$2.50

Washington Park

ARBORETUM BULLETIN

Published by the Arboretum Foundation
for the University of Washington
Vol. 50, No. 2, Summer 1987

Pollen!

Concerning This Issue . . .

Pollen!

The topic of the season — at least here at the Bulletin. Thanks to the participation, support, and planning of many people, we have an issue dealing with many facets of pollen and pollination. Hayfever, archaeology, alpine ecology, birds! In fact, we have so much material that it fills this issue and spills into fall. Stay Tuned!

Bastiaan J.D. Meeuse

The major inspiration and driving force behind this issue has been Professor Bastiaan J.D. Meeuse — Bas to his friends — of the Botany Department of the University of Washington. He has been on the Editorial Board of the Arboretum Bulletin since 1972, and has contributed articles as far back as 1959. Dr. Meeuse was born in the East Indies, spent some of his years growing up in West Java, was educated at the Universities of Leiden and Delft in the Netherlands, and taught his first class on pollination at the UW in 1957.

He truly is our resident expert on the subject of pollen. He has written much in this area, his best known work possibly being *The Story of Pollination* (Ronald Press, 1961), and his most recent is *The Sex Life of Plants* (Facts-on-File, 1984), reviewed on page 28 of this issue. This last volume evolved with a film for television, *Sexual Encounters of the Floral Kind,* (recently seen locally on the KCTS show *NATURE*), that Dr. Meeuse made with Oxford Scientific Films.

Bas was instrumental in rounding up articles and providing guidance for this issue, which was inspired in part by the photos by scanning electron microscope taken by Dennis Kunkel, and also by the recent growing interest in pollen counts, given by the TV weathermen, of particular interest to hayfever sufferers. So, on behalf of the Arboretum community, I thank him for his contribution this last year while this particular Bulletin was in preparation, and for his years of valuable participation.

Now, enjoy!

Palma Hoppel
Editor

The ARBORETUM BULLETIN is published quarterly, as a bonus of membership, by the Arboretum Foundation, a non-profit organization to further the development of the Washington Park Arboretum. Information regarding membership in the Foundation may be obtained by writing to the Arboretum Foundation, University of Washington XD-10, Seattle, WA 98195 or by calling (206) 325-4510. Articles on botany and horticulturally-related subjects written by professional and amateur botanists, horticulturists, educators and gardeners are welcome. No part of the BULLETIN may be reprinted without the authority of the Arboretum Foundation. Typesetting by Scarlet Letters, Ltd., production by Palma Hoppel, lithography by United Graphics Printers.

The Washington Park

Arboretum Bulletin

VOLUME 50, NUMBER 2, SUMMER 1987

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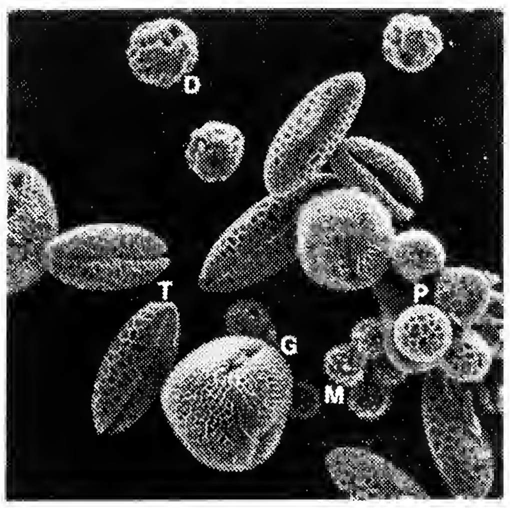

THE COVER

A photo of pollen made with a scanning electron microscope by Dennis Kunkel. The photo is 860 times life size and the specific pollen grains are as follows: D—dandelion; G—geranium; M—marigold; P—phlox; T—tiger lily. See the article on page two for more information.

Pollen Grains by Electron Microscope

DENNIS KUNKEL & BASTIAAN J.D. MEEUSE

Throughout this issue you will find amazing photos of pollen grains. They were taken using a scanning electron microscope at the University of Washington Botany Department by Dennis Kunkel. Simply stated, the pollen grains were carefully dried, coated with gold/palladium (making a conductive surface and secondary electron source), and put in the scanning electron microscope, and bombarded with electrons. As primary electrons struck the surface of the pollen (actually the coating), secondary electrons were produced, and these were translated into an image and viewed on a CRT (cathode ray tube). With this particular type of scope, the surface of the specimen can be scanned and magnified (thousands of times), making it a "scanning" electron microscope. A special Polaroid camera takes photos directly from the CRT screen. Each photo has a guide to its size in microns; a micron being one thousandth of a millimeter, or one millionth of a meter.

For those interested in identifying pollen, the following books are strongly recommended:

Brown, C.A. 1960. *Palynological techniques.* Baton Rouge, Louisiana: no publisher given.

Erdtman, G. 1952. *Pollen morphology and plant taxonomy.* Angiosperms: An introduction to palynology, vol. I, pp. XII + 1-539. Stockholm: Almqvist & Wiksell; Waltham, Massachusetts: Chronica Botanica.

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_____. 1965. *Pollen and spore morphology/plant taxonomy.* Gymnospermae, Bryophyta (text), pp. 1-191 and 24 plates. Stockholm: Almqvist & Wiksell.

_____. 1969. *Handbook of palynology. Morphology, taxonomy, ecology*, pp. 1-486. Copenhagen: Munksgaard.

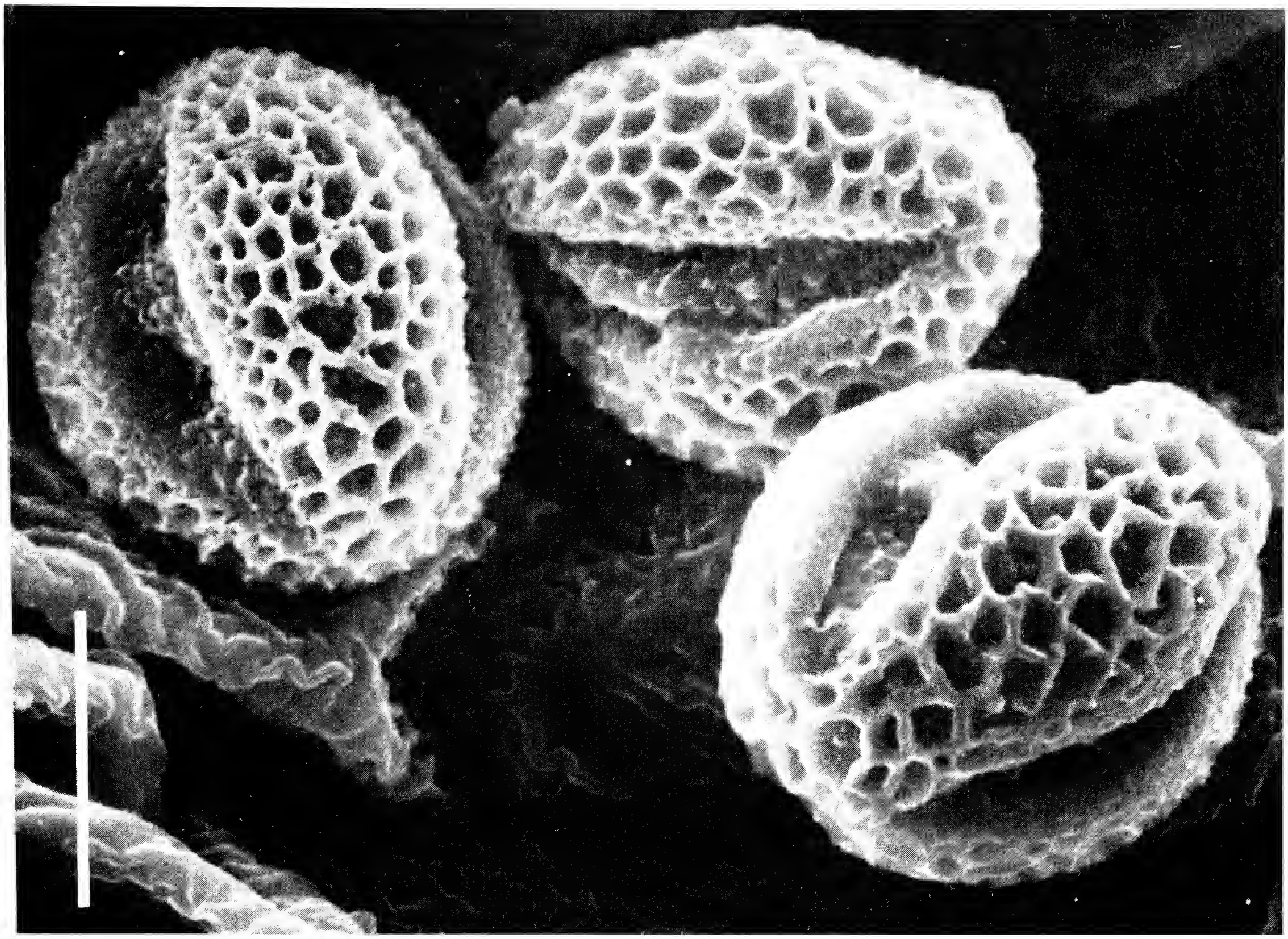
Faegri, K., and Iversen, J. 1950. *Textbook of modern pollen analysis*, pp. 1-168. Copenhagen: Munksgaard.

Kapp, R.O. 1969. *Pollen and spores*. Dubuque, Iowa: Wm.C. Brown Company.

Kremp, G.O.W. 1965. *Morphologic encyclopedia of palynology*, pp. 1-186 and 38 plates. Tucson, Arizona: University of Arizona Press.

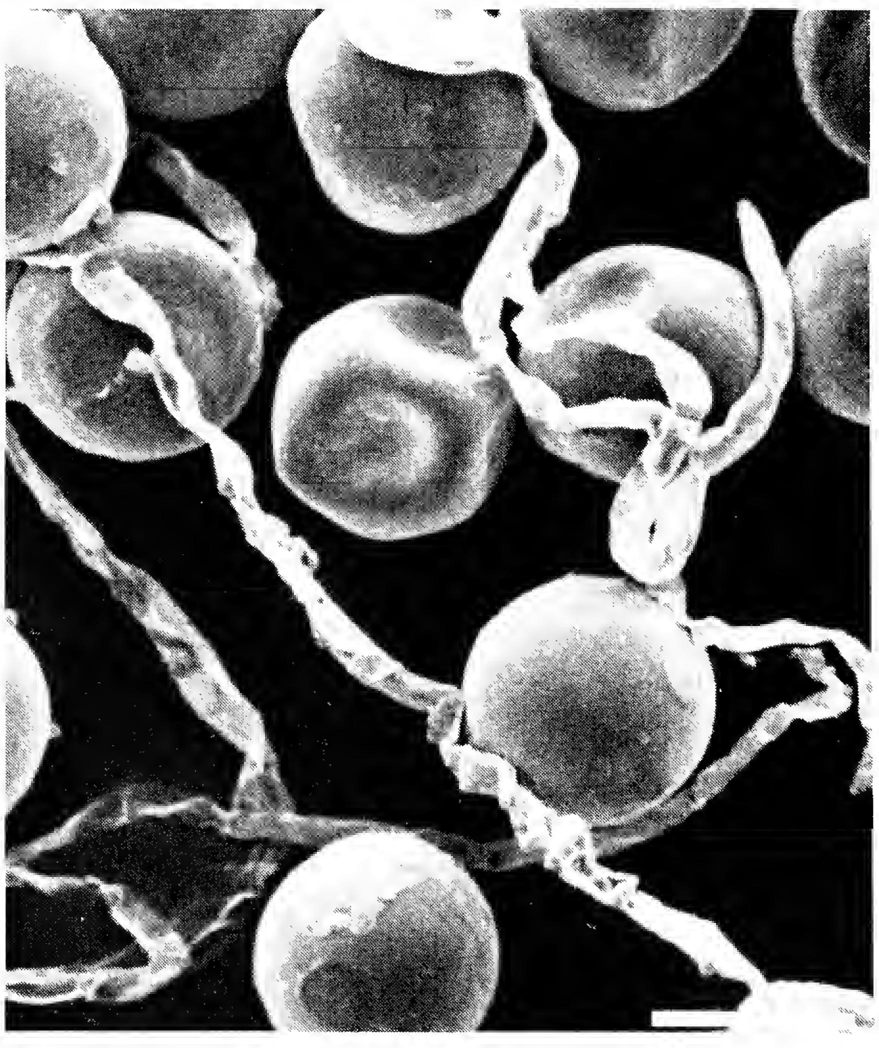
Moore, P.D., and Webb, J.A. 1978. *An illustrated guide to pollen analysis*, pp. 1-133. New York: John Wiley & Sons.

Wodehouse, R.P. 1953. *Pollen grains, their structure, identification and significance in science and medicine*, pp. XV + 1-574. New York: McGraw Hill.



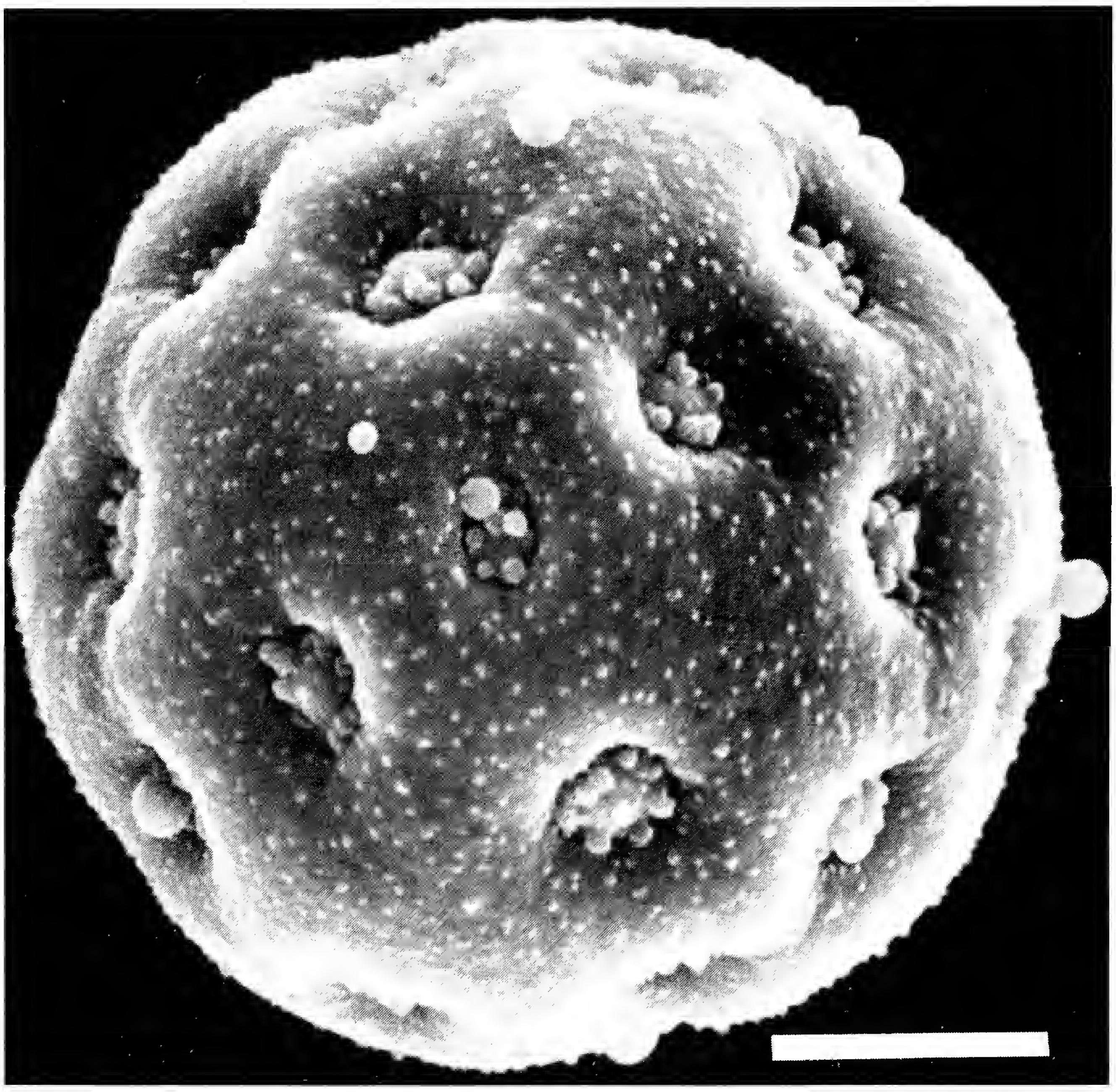
Pollen grains of a willow, Salix, *still in the anther. Within the genus, we find both wind pollination and bee pollination. Willows are dioecious, and the presence of honeybees or bumblebees on the male catkin in early spring does not necessarily mean that there is cross pollination, since the insect visitors, displaying floral constancy, may stick to the same tree. (Bar = 10 microns)* *photo: Dennis Kunkel*

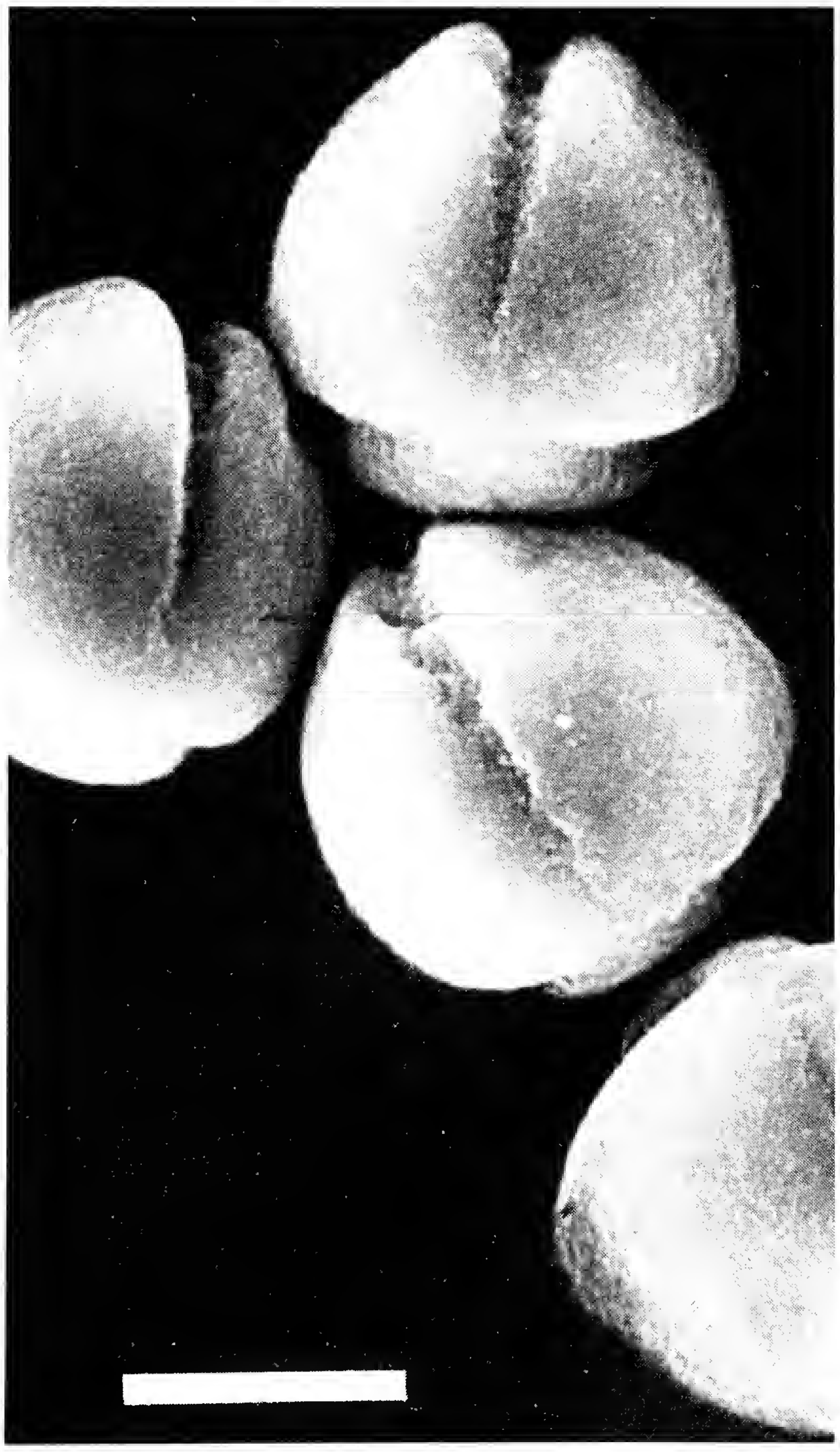
Pollen of a milkweed, Asclepias. *(Bar = 500 microns).* *photo: Dennis Kunkel*



Pollen of an evening primrose, Oenothera biennis, *a hawkmoth-pollinated species. The grains are connected to one another by sticky threads. (Bar = 50 microns)* *photo: Dennis Kunkel*

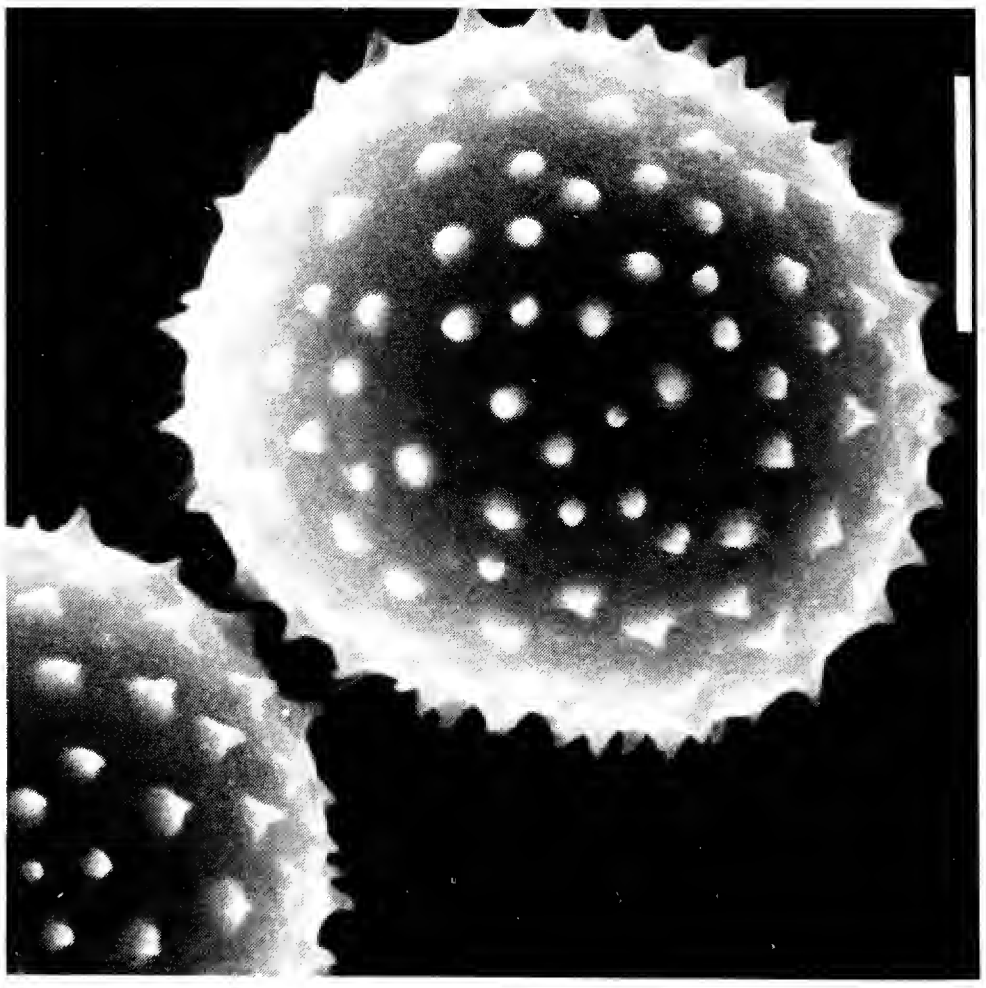
Pollen of a morning glory, Convolvulus, *a hawkmoth-pollinated plant. (Bar = 20 microns)*
photo: Dennis Kunkel





Pollen of European bittersweet, Solanum dulcamera, *now a common weed in the U.S. Bumblebees shake the grains out of the anthers by buzz pollination, and this pollen (powdery and dry), therefore, has all the characteristics of a wind-borne one. (Bar = 2 microns)*
photo: Dennis Kunkel

Pollen of voodoo lily, Sauromatum, *dispersed by beetles and large flies. (Bar = 10 microns)* *photo: Dennis Kunkel*



In The Arboretum

After 32 years of dedicated service to the Arboretum, Richard Hart, Grounds Supervisor, has retired. Dick will still be with us on Wednesdays and Thursdays helping with special projects.

The major emphasis of activity for early summer has been irrigation. Troubleshooting automatic systems and fine-tuning manual irrigation practices is an ongoing concern. The emphasis this year will be on monitoring soil and plant conditions and thorough but less frequent waterings.

Just as summer seems synonymous with irrigation, so does it promise the appearance of "Herb Robert" (*Geranium robertianum*). The staff has been hard at work with the endless task of shrub-bed weeding and greatly appreciates the help of volunteers in the summer Heather Bed, Loderi Valley, and on the Memorial Hillside. Several landscape projects received the staff's attentions, including partial renovation of the bank between Foster Island and the service yard.

Pruning activities have centered around the cherries on Azalea Way and the plantings at the lower Woodland Garden pond. Brush generated is chipped and used as mulch.

The Arboretum Greenhouse/Nursery operation is still going through a major phase of transition with the renovation of the greenhouse. Plants along the south wall were removed, several taking up residence in new beds around the maintenance building. Renovation of the lathhouse plantings also has been a primary focus. A large number of plants were dug and prepared for the CUH shade garden.

Also completed was the cosmetic improvement of the landscape around the Donald G. Graham Visitor's Center. Landscape bark was spread and a lath fence now screens the construction zone from view. Unit 41 of the Arboretum Foundation designed the raised planter on the west side of the building and planted it with annuals provided by the Unit Council. Hanging baskets are in place and the half-barrel planters are overflowing. Hand mowing and fertilizing are improving the quality of the turf.

Turf care, especially mowing, consumes a great deal of the Park's crew's time in early summer. In an effort to reduce the volume of grass clippings left behind and the incidence of scalping, mower cutting height has been raised one-half inch on a trial basis.

Bob Baines
Park's Crew Supervisor

Airborne Pollen and Hayfever

LISA SCHNELL AND BASTIAAN J. D. MEEUSE

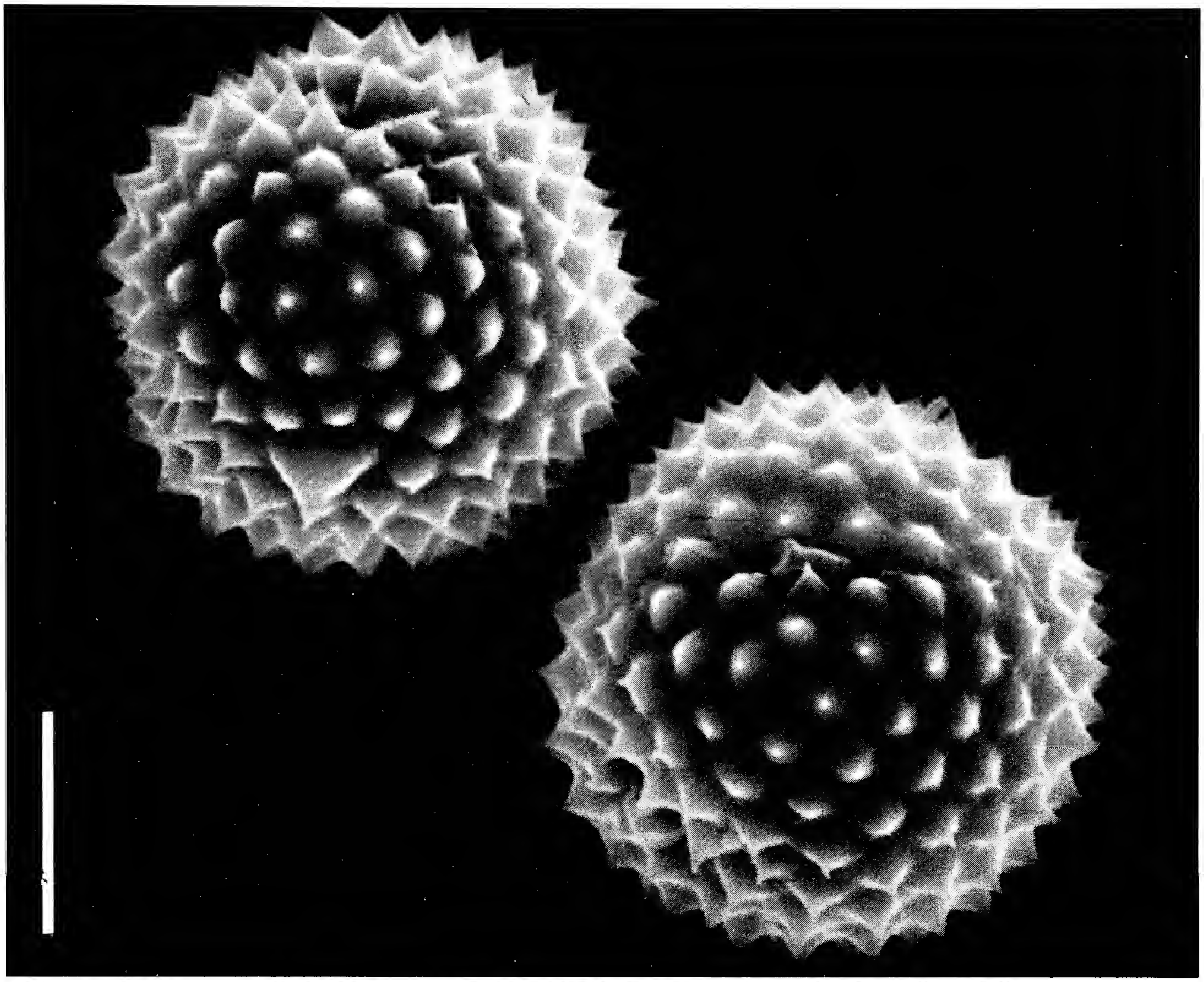
What's in a name?

It is common knowledge that hayfever is a most irritating affliction that affects millions of people worldwide. Its annual cost in the form of medical expenses and lost wages amounts to millions of dollars. The name of this affliction is actually misleading; the only justification for it is that most victims of hayfever develop their symptoms in early summer when the grass in the meadows is ready to be cut. After Bostock's classic publication on the subject in 1819, people in Europe began to realize that the real culprit is pollen (often grass-pollen) and not hay. Especially in medical circles the name ''pollinosis'' has become popular, but it too has its disadvantages because it leads to the unwarranted belief that a person has to *breathe in* airborne pollen to become sick. In reality, there are plenty of people who develop unpleasant symptoms after oral ingestion of pollen!

Hayfever *or* pollinosis, the name simply represents a violent allergic reaction of the whole human immune system to certain substances, usually proteins, bound on the surface of pollen grains. The two requirements for hayfever are, therefore: a) a sensitized individual, and b) enough pollen to alert the body's immune response. Hayfever must never (NEVER!) be underestimated. Much more is involved than sneezing and itchy eyes! One of the very best tests for hayfever nowadays is the so-called ''thrombopenic index'' test developed by Storck; it's based on the fact that the number of blood platelets or thrombocytes in the blood of hayfever victims drops significantly. Hayfever also has a strong effect on human ovulation, and in sensitized women this can lead to a temporary loss of fertility (Schata and coworkers, 1983).

Hayfever plants

Not surprisingly, most hayfever-causing plants are wind-pollinated species such as grasses, plantain, ragweed, hazel and alder. All of these produce tremendous amounts of pollen as part of their pollination strategies. We must, however, be on guard against overgeneralization. In principle, insect-borne pollens are just as allergenic as wind-borne ones, and they too will sometimes become available in large quantities. In horse-chestnut (*Aesculus hippocastanum*) the pollen grains possess spines and are very well suited to insect pollination (which is the rule here). However, they also happen to



Pollen grains of ragweed, Ambrosia artemisiaefolia, *probably the most notorious hayfever plant of all.*
(Bar = 10 microns) *photo: Dennis Kunkel*

be very light, and become airborne very easily. During the blooming season, horse-chestnut pollen can be found in collecting devices—usually placed atop tall buildings—side by side with pollen from grasses and other "classically" wind-borne pollens. Complaints from people who claim that pollen from *Cytisus scoparius* (Scotch broom) and other *Cytisus*-species (typical bumblebee-pollinated plants) gives them hayfever must be taken seriously: the pollinating bumblebees cause the young and still unopened flowers to "explode," releasing small clouds of pollen into the air.

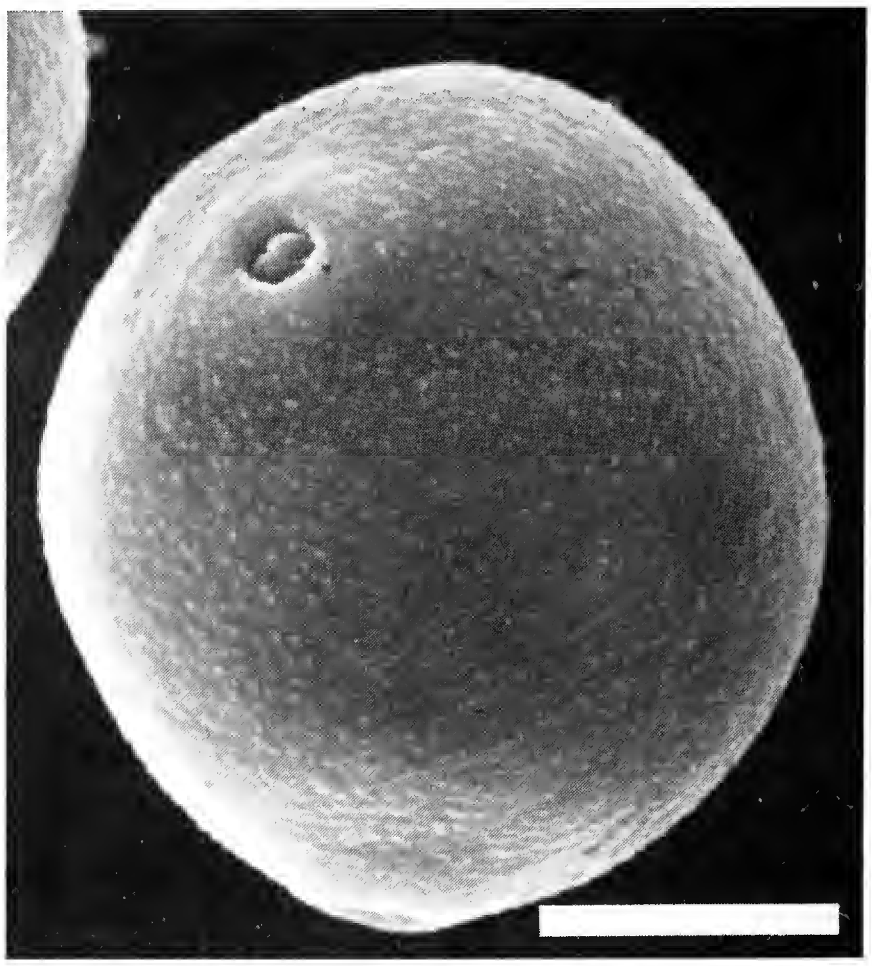
Pollen identification

Referring the reader to the article by Kunkel and Meeuse, in this issue, for pollen-grain illustrations, we will in our present article try to illuminate the botanical aspects of hayfever, contrasting wind pollination (anemophily) and animal pollination (zoophily). Basic to our understanding is the knowledge that pollen grains are highly characteristic for the particular plant species that produce(d) them. Under the microscope, they can be identified with great ease, and they are therefore to the botanist what fingerprints are to the criminologist.

How much pollen is produced?

As already mentioned, anemophilous plants usually produce pollen grains in huge numbers; a single inflorescence of sorrel (*Rumex acetosa*) may produce 400 million of them, one cattail inflorescence (*Typha angustifolia*) 175 million. Fritz Knoll has estimated that 600 million pollen grains are produced by an average hazelnut bush. What *really* counts, however, is the number of pollen grains available for each ovule (or prospective seed). In hazelnut, it amounts to about 250,000. Judged superficially, this looks like overkill. In actual practice, however, we find that the population density of the pollen grains in the immediate vicinity of the ovules remains very low, and this observation has interesting implications as far as the number of ovules per pistil (that is, the number of seeds per fruit!) is concerned. It is all a matter of logistics.

The production of pistils and ovules represents a certain investment of resources on the part of the mother plant; it is an "expensive" proposition, and the plant must use its investment as wisely as possible. Of course it is important for a plant to leave as much offspring, in the form of seeds, as possible, but what is the best way to achieve this end? Should the plant produce one pistil or a very few pistils, each with a large number of ovules, or should it follow the opposite strategy of producing a fairly large number of pistils, each with just one, or a very few, ovules? The answer can be found through the following reasoning. The chance for a pistil to be hit by a falling pollen grain is very small; the chance to be hit by two grains in succession is extremely small, and the chance to be hit three times is almost negligible. To put many ovules in a pistil would therefore be very wasteful; most of them would remain unfertilized for lack of the corresponding pollen grains! Clearly, the best strategy is to produce a fairly large number of pistils, each with only one ovule. This is indeed what we observe; each hazelnut has only one seed (rarely two). In animal-pollinated flowers, the pollen grains do not arrive one by one, but in groups or clumps (since the pollinator transports them that way). Here, we normally find many seeds per fruit; up to a million in certain orchid flowers (*Vanilla*), several thousand in the case of European poppies (*Papaver*). Very illuminating, in this context, is a comparison between *Papaver* and the wind-pollinated *Bocconia,* which is in the same family, but has only one seed per fruit.



Pollen of a hazel species, Corylus. *In this plant, the pollen grains outnumber their female counterparts (the ovules) about 250,000 to one. (Bar = 10 microns)*
photo: Dennis Kunkel

Characteristics of wind-dispersed pollen grains

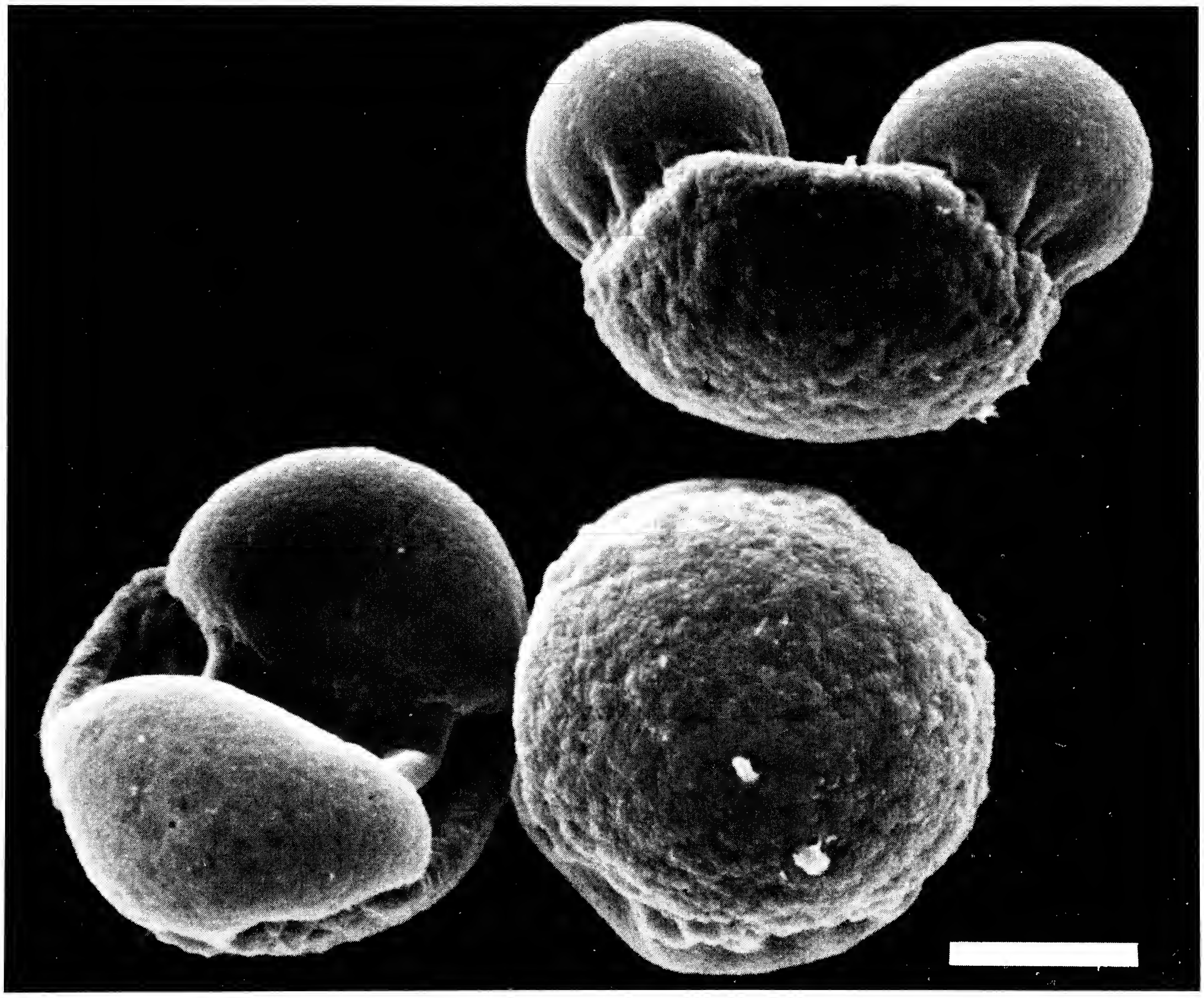
Wind-dispersed pollen is a dry, light, flour-like powder, composed of grains that lack the stickiness which holds insect-borne pollen grains together. The outermost layer of the grains is smooth and completely devoid of spines, warts or other adornments. Liberated from the anther, it quickly loses water so that it becomes much lighter. The capacity to float in the air depends partly on the speed of the wind and partly on the speed with which the pollen grain itself would fall in still air. That speed is controlled by Stokes's law, which states that the

Hazel catkins. *photo: Tom Boyden*

smaller the diameter and the less the specific weight of a spherical body, the greater is the resistance of air to its fall. It is even possible for a body to be so small that its rate of fall equals zero so that it will float in the air continuously—as particles of dust or drops of mist do. Not surprisingly, the biggest and heaviest pollen grains are found in animal-pollinated plants; e.g., those of pumpkin (*Cucurbita pepo*) have a volume of about 0.5 mm^3, weigh about 0.001 mg each and will fall in still air with a speed of one foot per second. For wind-pollinated plants in general, comparatively low rates of fall (of about one inch per second) are found. The low rates for pollen grains from conifers such as Scots pine, silver fir, spruce and true cedar (*Cedrus*) seem surprising in view of the fact that these grains are among the heavier ones; however, each one has two little airsacs which lend them an odd Mickey Mouse appearance but increase their buoyancy. Horse chestnut, although insect-pollinated, is exceptional in that its pollen grains are a thousand times lighter than those of pumpkin, and have a rate of fall of only 0.25 cm (or 0.1 inch) per second.

Pollen as "aerial plankton"

Pollen grains floating in the atmosphere can legitimately be compared with the millions and millions of small organisms (such as diatoms and microscopic algae) found in oceans and lakes, and collectively known as plankton; hence the term "aerial plankton." Wind-pollinated plants liberate their pollen with remarkable regularity at definite times of the day. In alder, for instance, it is released just after midday, around 2 p.m., when the temperature is at its highest and the humidity at its lowest, while a slight breeze may also be in evidence. Pollen may then be carried to a



Pollen of a true cedar, Cedrus deodara *Notice the air sacs, which help to keep the pollen afloat. (Bar = 20 microns)*
photo: Dennis Kunkel

height of several thousand feet by ascending air currents. Above the Mississippi basin, it was shown to be present at an altitude of 19,000 feet. In Europe, pollen has frequently been collected at heights between 6,500 and 10,000 feet with the aid of airplanes and hot-air balloons (Linskens and Jorde, 1986). The greatest abundance is found between 300 and 1,500 feet. The higher the pollen goes, the more likely it is that it will travel over considerable distances. According to the German scientist H. Rempe, any pollen reaching an altitude of 6,500 feet is likely to cover a distance of 190 to 250 miles during 24 hours, even at the moderate wind velocity of 10 miles per hour.

The "rain of sulphur" which falls on the north side of the Alps is known to be caused by pollen from coniferous forests in northern Italy. In the U.S., "sulphur rains" are greatly in evidence in early summer on Crater Lake, Oregon. On the University of Washington campus, they can be observed in late autumn, when the Himalaya cedars (*Cedrus deodara*) are shedding their pollen. It has been calculated that in Central Europe about 11,000 pollen grains coming from trees fall on every square centimeter during the course of the year. If pollen from herbaceous species had been taken into account, the total figure certainly would be much higher, probably around 27,000.

The biological importance of long-distance pollen dispersal has been demonstrated very elegantly by Rempe, who took advantage of the fact that the North Sea island of Heligoland, about 30 miles from the European mainland, is almost totally devoid of wind-pollinated trees. It was on its 150-feet tall cliffs overlooking the North Sea that Rempe, in the spring of 1934, set up his pollen-collecting apparatus. It consisted of brass tubes measuring 45 by 14 millimeters. Their cylindrical shape was much more similar to that of a flower's stigma than a flat glass plate would have been, and they had the significant additional advantage of always exposing a similar receptive surface to the wind, whatever its direction. Each tube was covered with cellophane smeared with Vaseline so that any pollen carried by the wind would stick to it. After having been exposed over a standard period of time, the cellophane was peeled off and examined under a microscope to determine the number and type of pollen grains per unit of surface area.

After 24 hours of exposure to easterly, northeasterly and southeasterly winds, pollen grains were found to be present on the cellophane in the following proportions: pine, 30.4%; oak, 41.7%; birch, 4.2%; spruce, 0.9%; grasses and sedges, 0.4%; other plants, 16.4%. The absolute number for the pollen grains of oak, collected over a 3.5 day period, was 955. If the size of the receptive cellophane surface had been equal to that of a stigma of pedunculate oak (*Quercus pedunculata*), that is 0.8–1.0 square millimeters, the number would have been 10. The experiment clearly shows that an oak tree separated from others by a distance of some 30 miles is certain to be pollinated (during a 3.5-day period). Whether or not this would result in the formation of viable seeds is still a matter of debate, since during a long air-trip at high altitudes pollen is likely to suffer adverse effects from the sun's ultraviolet rays. On the other hand, it should be kept in mind that pollen also travels at night when UV rays are not in evidence. Indeed, a lot of it comes down at that time. In the early morning hours Rempe found only small amounts of pollen at heights exceeding 1,500 feet.

In the City of Seattle, monitoring of the air quality in terms of pollen is now done on a regular basis as a public service to the citizens—more specifically, of course, to those of us who suffer from . . . HAYFEVER!!!

Epilogue

In the above, we may have given the impression that wind pollination always is an extremely wasteful and random process. Recently, however, Karl Niklas has brilliantly demonstrated that there still can be system in Mother Nature's madness! Careful aerodynamic analysis of the wind-flow patterns around such highly structured objects as, e.g., pine cones reveals that the pollen grains are actually *guided* towards the places where they can do the most good: the ovules or prospective seeds. In loblolly pine (*Pinus taeda*) it has been calculated that on the average about four pollen grains are made available to each ovule. This could impress one as a slight overkill, until it is remembered that in coniferous plants the ovules contain several egg cells each, and not just one as in the flowering plants. The ratio of pollen grain to egg cell in loblolly pine is, therefore, nearly one-to-one. Of the embryos formed, only one will survive, presumably the one with the best genetic endowment. Clearly, Nature in this case exerts "quality control" at the embryo stage rather than through pollen as it does in the flowering plants.

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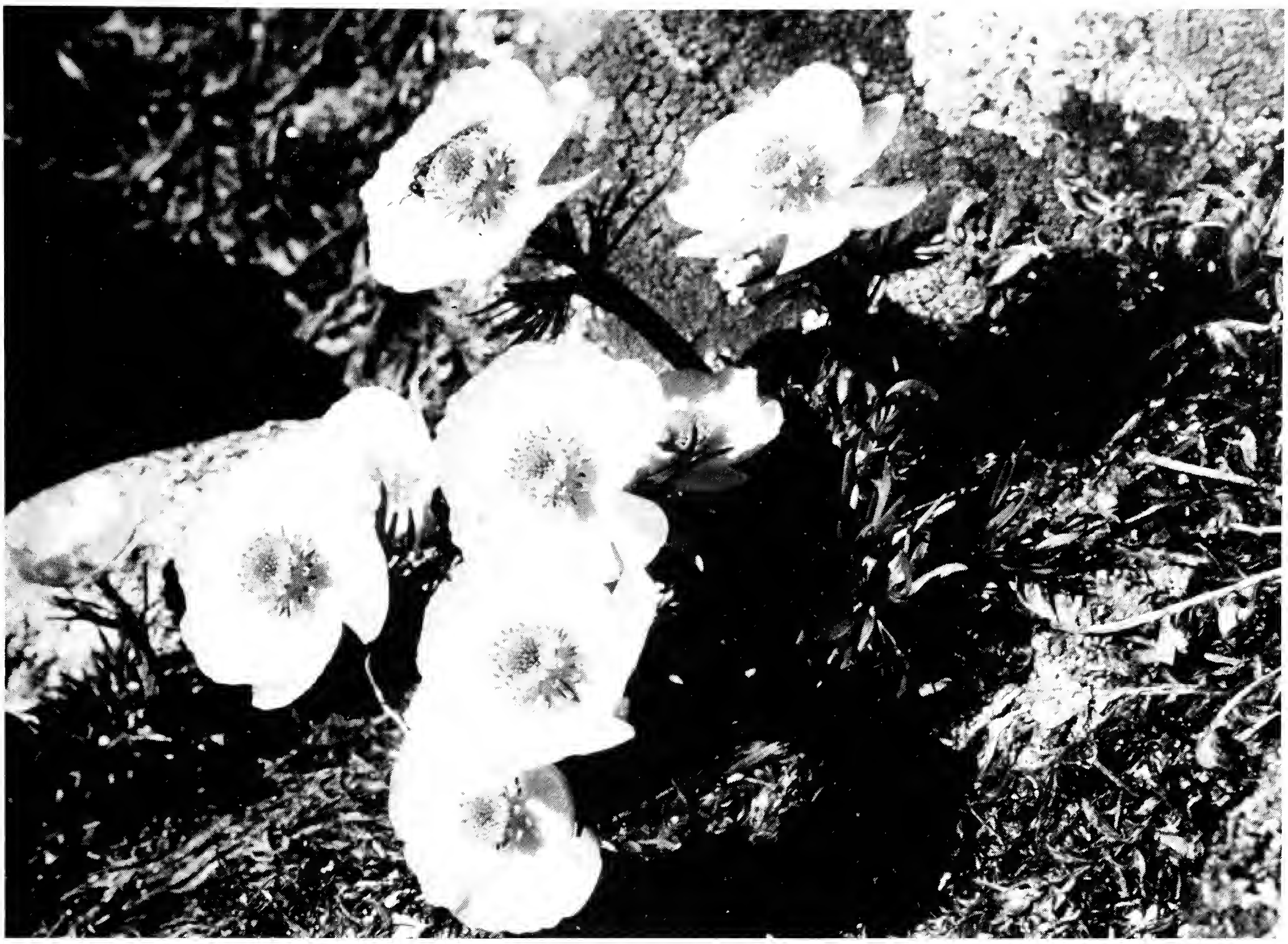
Pollination Ecology of Alpine Plants

RONALD J. TAYLOR

Professor of Botany, Western Washington University

The alpine zone is an area of contrasts. The growing season is short and generally cool; however, temperature fluctuations are extreme, varying as much as 50 degrees Fahrenheit (or more) within a 24-hour period. Freezing temperatures may occur on any given night during the summer months. Snow or sleet storms are not uncommon during the growing season, and the wind is usually blowing, often at gale force. Occasionally the air is still, the skies are clear, and the sun beams down with burning ferocity. The alpine plants are adapted to deal with the extreme variation of the climate and with soil instability. They are generalists in the sense that they have the phenotypic plasticity to bend with the environment but there is little give in the reproductive process. Flower development, pollination and seed production are critical stages in the life cycle of plants. Therefore, alpine species must have pollination strategies that ensure reproductive success. Pollinating animals (mostly insects) must contend with these same stressful conditions, either by adaptation or avoidance, or a combination of both. It is not unusual for periods of several days to pass during which time insects cannot forage (and plants cannot be pollinated) because of inclement weather.

Several studies dealing with alpine pollination ecology have listed insect groups according to their importance as pollinators. Although the order of importance varies according to the area studied, most of the same groups are regularly listed. The insects that most consistently show up on these lists are: bumblebees, syrphid flies, muscid flies, and butterflies. Less regular pollinators include dance flies, mosquitoes, solitary bees, and an assortment of beetles. In North American alpine environments, including the Cascade Range, bumblebees appear to be the most important pollinators. Their importance is based on a combination of several characteristics: (1) they can thermoregulate, maintaining a thoracic temperature of about 90 degrees F, suitable for flight, even when ambient air temperatures are near freezing; (2) they can conserve energy by allowing their thoracic temperature to drop while on the inflorescence of a plant and then "warm up" again before flight; (3) queen bumblebees normally incubate their brood, providing protection against the low temperatures of the alpine environment; (4) bumblebee colonies are present throughout the flowering season, thus foraging on several



In Rainier National Park, an example of a bowl-shaped flower, Ranunculus eschscholtzii. *photo: author*

species of plants during the summer; (5) bumblebees feed only on floral rewards, requiring them to visit numerous flowers in an "outing"; (6) bumblebees have large individual energy requirements and have to carry food home to a hungry brood, again requiring them to visit numerous flowers.

The bumblebee colony as a whole assumes a generalist role in pollination, since a wide variety of plant species is visited. However, individuals tend to specialize, or major, on one or two species at any given time, and minor on other, less rewarding species. The minors serve as bridges to new majors when the previous majors are no longer available. In the selective process of majoring, several flower types may be explored with the species providing the greatest reward being selected. The ability to discriminate among flowers and thus major is essential for bumblebees to meet their considerable energy requirements, especially in an alpine environment.

Flowering phenology is important to pollinators because it determines the pattern of resource availability. The variety and density of plants flowering at any one time also have a direct effect on pollinator diversity and abundance. Phenology is controlled primarily by climate but in the alpine zone it is closely linked with the pattern of snow accumulation and release. Even though within any plant community the flowering periods of individual plant species overlap and form a continuum, the plants do follow a flowering sequence. It has been theorized that the divergence of flowering times in a community is the result of competition for pollinators, as well as time of release from snow. When two plant species that flower synchronously depend upon the same insects for pollination, reproduction by one or both species may be adversely affected. Competition could then function as a selective force to cause separation of flowering periods. Competition could also be a force in the evolution of specialized floral morphologies and the development of reproductive strategies not requiring visitation by pollinators. On the other side of the coin, however, is the argument that there is selection for synchronous flowering of plants with the same pollination strategy. The result would be a higher density of flowers in the mixed stands and a greater attractive force for selected pollinators with all involved species sharing the wealth. The third obvious alternative is that there is no functional relationship between flowering phenology and pollinators. In alpine communities, supporting evidence can be found for all of these hypotheses.

Pollination Strategies of Alpine Plants

Agamospermy—Agamospermy is the process by which seeds are produced without fertilization (seeds without sex). Therefore, there is no genetic recombination, no genetic variation within a population except through mutation. Technically, this is not a pollination strategy except that pollination may stimulate seed production. At first glance this type of reproduction would seem to be disadvantageous since there is little opportunity for environmental adaptation. Two major advantages of agamospermy are that: (1) plants can flower early in the season or during inclement weather when pollinators are unavailable, the insecurity of pollination and sexual reproduction thus being alleviated; (2) adaptive combinations of genes, including those of sterile hybrids, can be perpetuated indefinitely, yet the plants have the advantage of dispersal by seeds. An example of an agamospermic species in the Cascade Range is *Draba paysonii.* This is a common alpine cushion plant with attractive yellow flowers. It is infrequently seen in flower because of its very early flowering period.

Anemophily (wind pollination)—Although wind pollination represents the shotgun approach to pollen dispersal, and massive amounts of pollen must be produced at considerable energy expense to ensure fertilization, it may be adaptive under certain conditions. The most critical of these is that wind-pollinated species must occur in sufficiently large populations that there is a reasonably good chance of pollination success. Given this, two advantages of anemophily are: (1) wider range of pollen dispersal, resulting in a larger gene pool and, accordingly, greater genetic variability and adaptive potential in the breeding population; (2) freedom from dependency on animal pollinators which may not be around when needed, in contrast to the ever-present wind. Wind pollination is the strategy used by some of the most abundant and ecologically important species of alpine communities, the graminoids, i.e., grasses, sedges and rushes. These plants have small reduced flowers that are structured to efficiently disperse and capture wind-blown pollen. The sequence of floral development usually ensures cross-pollination rather than selfing. This is often achieved by maturation of stamens before the stigmas become pollen-receptive. In some taxa (e.g., sedges), flowers and often entire plants are unisexual. If plants were able to be self-fertilized, the major advantage of wind pollination—the facilitation of genetic variation and resulting adaptive potential—would be lost.

Entomophily (insect pollination)—One of the most striking examples of coadaptation is that of insects and the flowers they visit. Although the alpine flora is not as varied as that of most vegetative provinces, coadaptation is well exemplified and most classes of floral morphologies that have traditionally been associated with particular pollinators are equally evident here. Alpine flower types, treated as pollination units, are presented and discussed below.

A wind-pollinated sedge, Carex albonigra. *photo: author*

Dish- or bowl-shaped flowers

Species with this floral morphology have radially symmetrical flowers with a generalist pollination strategy. The floral rewards are easily available to essentially all types of visitors, from the most primitive (beetles) to the most advanced (bumblebees). The obvious advantage of this morphological strategy is that some types of would-be pollinators are almost always present. However, many of these insects are inconsistent pollinators at best. These flowers usually have low nectar rewards and are visited by such specialists as bumblebees only as a last resort (as minors), except when the bees are foraging for pollen. Alpine generalists have bright colored flowers, usually yellow, or white. Attesting to the success of this strategy, the large majority of alpine entomophilous flowers are yellow or white generalists. Plant families well represented in the alpine and utilizing the generalist strategy include: Rosaceae, especially *Potentilla* spp.; Saxifragaceae, especially *Saxifraga* spp.; Caryophyllaceae, especially *Cerastrum* and *Arenaria* spp.; Ranunculaceae, especially *Anemone* and *Ranunculus* spp.; Cruciferae, especially *Draba* and *Erysimum* spp.; and Crassulaceae, *Sedum* spp. Many species of Compositae may be considered to be generalists, even though the individual flowers have short tubes. Perhaps the most important pollinators of generalist flowers are the fair-weather syrphid flies. These and other visitors move about in a way termed ''mess and soil,'' collecting pollen on various parts of their bodies.

Brush-type flowers

In these flower types, stamens or styles extend beyond the perianth (sepals and/or petals), and the flowers are densely clustered. The result is an attractive inflorescence resembling a giant caterpillar. These flowers are visited primarily by bumblebees foraging for either pollen or nectar or syrphid flies feeding on pollen. Two families with this type of pollination unit and well represented in the alpine are Hydrophyllaceae, *Hydrophyllum* and *Phacelia* spp.; and Polygonaceae, *Polygonum* spp.

Trumpet- and tube-shaped flowers

These flower types are specialized for pollination by long tongued insects and hummingbirds. The petals and/or sepals are fused to form a tube with the nectar concealed at the base and accessible only to other butterflies and moths, bumblebees, and hummingbirds. Other insects, such as syrphid flies, may collect pollen when readily available. Flower color varies; butterfly flowers tend to be pink to lavender, bumblebee flowers blue, hummingbird flowers

Mountain heather, Phyllodoce glanduliflora, *a tube-shaped flower.* *photo: author*

A gullet-type flower, Mimulus tilingii. *photo: author*

purple to red, and yellow is a neutral color visited by all insects. The pollination strategy associated with this flower type is well represented in the alpine and several families are involved, including: Polemoniaceae, especially *Phlox* and *Polemonium* spp.; Boraginaceae, *Eritrichium;* Onagraceae, *Epilobium* spp.; Caryophyllaceae, *Silene* spp.; Ericaceae, various heathers and *Vaccinium* spp.; and Compositae with numerous species. The inflorescence of Compositae resembles a single generalist flower and may be visited by a large variety of insects, especially if the floral tubes are shallow or if the forager is collecting pollen.

Flag-type flowers

Alpine plants with flowers of this type are primarily found in the legume family (Leguminosae). The flowers are bilaterally symmetrical with the upper petal enlarged, often distinctly marked, and generally conspicuous. Floral rewards are concealed by the lower petals (the keel) and are available only by manipulation, mostly by bumblebees. Floral colors are typically blue to lavender or yellow. Common alpine representatives include species of *Lupinus, Oxytropis,* and *Astragalus.*

Gullet-type flowers

These are stereotypic bumblebee flowers. They are bilaterally symmetrical with a landing platform. The throat of the corolla tube (formed from the fused petals) is inflated, enabling the bumblebee to crawl into the flower some short distance before probing downward to the base of the tube to extract nectar. The shape and color pattern of the flower directs the bee to enter the flower in a repeatable way. Thus pollination becomes precise. The figwort family (Scrophulariaceae) typically has gullet-shaped flowers and is very well represented in the alpine. The most common genera are *Veronica, Mimulus, Penstemon,* and *Castilleja.* The latter two genera, especially the red- and purple-flowered species, are often visited by hummingbirds. Specialized pollination strategies, such as that involving gullet-shaped flowers, are very effective *if* the pollinators are available. In the alpine zone, bumblebees and butterflies are restricted more by cold and wet weather than are some flies, therefore specialization is a trade-off.

Most visitors to the alpine and subalpine zones are impressed with the brilliant and multiple colors of the wildflowers, and many are intrigued by the varied floral structures. But the beauty and fascination of our flora is greatly increased when flowers are viewed in the context of pollination units. The coadaptation between flowers and their pollinators is one of the wonders of nature.

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Book Reviews

The Year in Bloom: Gardening for All Seasons in the Pacific Northwest. Ann Lovejoy. 1987. Seattle: Sasquatch Press.

This book by a new young author is sweeping through Northwest gardening groups like a fresh spring breeze. Less than two years ago, Ann Lovejoy began writing professionally, producing a garden column for *The Weekly.* Her book is even better, and is both well organized and creatively presented. She uses the page margins to list plants found on those pages, as an aid to scanning, and ends the book with appendices and an extensive index of both common and Latin names.

This book is in no way intended as a landscaping design primer; in most instances it reflects her own garden, described by some as the epitome of an American version of an English cottage garden. Ann writes, "The gardener's relationship with his plants ought not to be combative; yet control, with the lightest of hands, is part of the art of gardening. The greatest control comes from the most intimate knowledge; when you know your plants, you don't ask them to do what they can't and you place them where they can readily do what they should do to best advantage. Result: a burgeoning living garden and a delighted and enthusiastic gardener."

The author tells of having bloom in her garden every day of the year and inspires fellow gardeners to go forth and do likewise. She speaks of alternatives to pesticides; of ferns as "fluffy understory"; and recommends edible landscaping for savory summer salads, exhorting us to "look through the garden with fresh eyes and start munching"—nasturtium flowers, hollyhocks, daylilies, pelargoniums, violets, and squash blossoms.

While the book describes a Northwest garden, and is written for a local audience, the love of gardening it expresses, and its commonsense approach, delightful style, and frequent humor give it universal appeal. I hope the subtitle and occasional local references do not limit its geographic distribution and appreciation.

Nan Ballard

The 60-Minute Flower Garden: Have a Yard Full of Dazzling Flowers in One Hour a Week. Jeff Ball and Charles O. Cresson. Rodale Press, Emmaus, Pennsylvania, 1987. 276 pp. Price: $13.95*
ISBN 0-87857-637-1.

This brightly covered 276-page soft-bound book presents the basics for *novice* gardeners who want an introduction to the design, establishment, and maintenance of herbaceous gardens. The book includes techniques for improving the soil and pest management.

The authors have designed several gardens–for either sun or shade–and listed the type of plants which could be used. The information is intended as a guide for someone who is just starting. The real mark of a gardener is when he or she adds the artist effect.

One interesting concept of the book is the method in which they group plants in order to balance a design. The reader learns how to add groups of plants according to height, color, and seasonality. They also stress the height of flower stalks versus actual plant (foliage) height.

This book complements the new video tapes and other references the authors have also produced. Mr. Cresson is an accomplished young gardener trained at Longwood Gardens, Royal Horticultural Society Garden at Wisley and Nemours. He presented one of our first public lectures recently at the Graham Visitor's Center.

If you have a friend who is just getting started, don't miss this one. If you are well beyond the "what should I plant" stage, go on to more advanced volumes.

John A. Wott
Professor of Urban Horticulture

* This book is available for use in the Miller Library, and for purchase in the Graham Visitor's Center gift shop.

Pollen and Archaeology

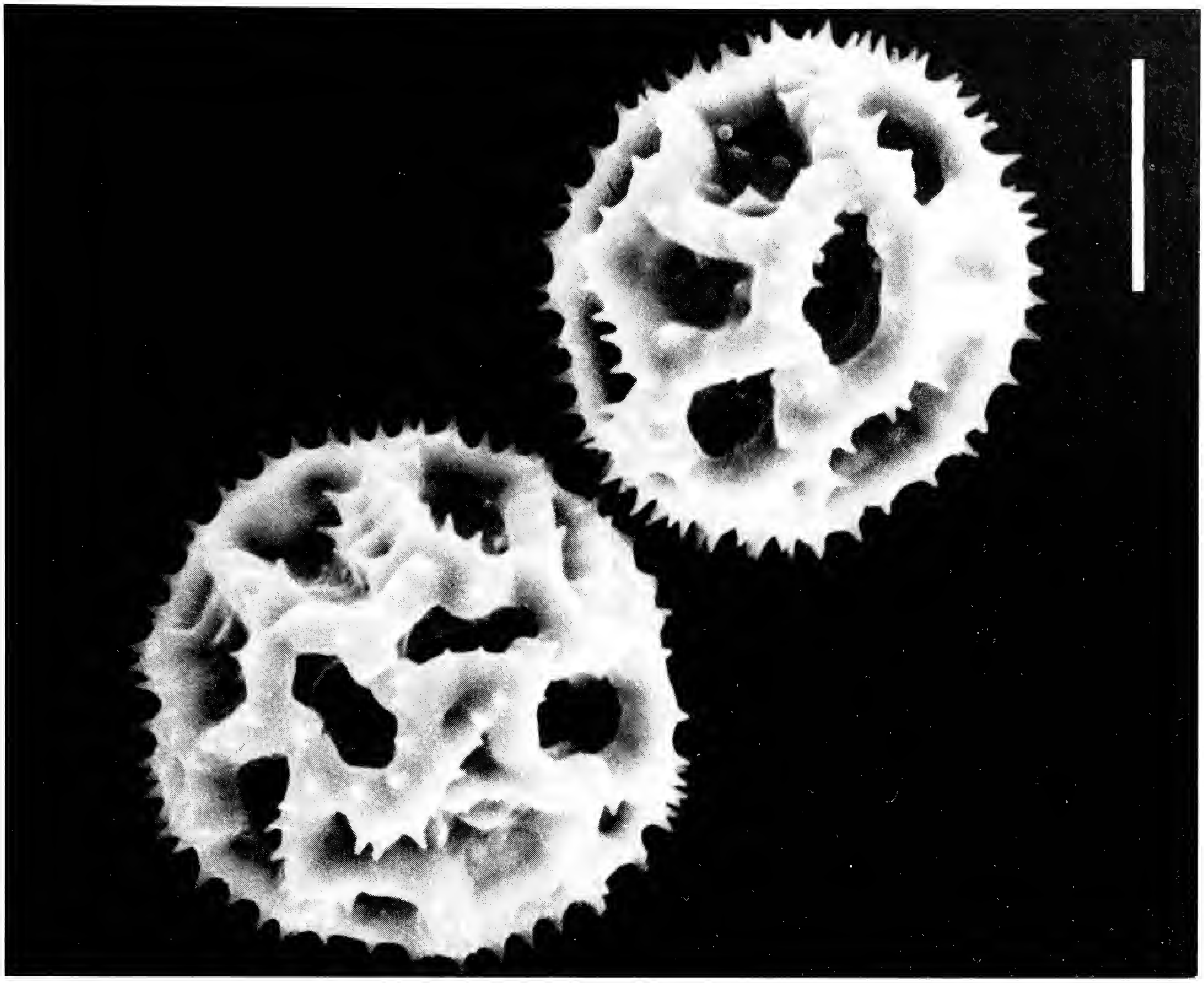
W. GEOFFREY SPAULDING

Geoffrey Spaulding is a Research Assistant Professor at the Quaternary Research Center and Department of Botany, University of Washington.

Palynology is the study of pollen and spores from living and fossil plants, and has applications in a diverse array of fields. For example, petroleum geologists use distinctive fossil pollen types to identify oil-bearing sediments in drill cores from deep within the Earth's interior. Paleoecologists use fossil pollen assemblages from ancient lake muds to reconstruct vegetation changes over thousands of years. And physicians and palynologists work in concert to identify those pollen types that are most likely to cause allergic reactions and, especially, to understand weather patterns and other environmental conditions that make some seasons, and some places, more troublesome than others to hayfever sufferers. Pollen is also of great use to archaeologists. To understand why, and how these minute particles are of value to those who study ancient cultures, we must first understand the nature of pollen.

A pollen grain is one of nature's remarkable constructs. It is a microscopic shell enclosing a bit of germ plasm, containing the male genetic information necessary for production of a fertile seed. Since plants do not move, they have evolved strategies to disperse their pollen so that it may reach other individuals of the same species. Those plants with attractive, showy flowers are animal pollinated, while those with simple, drab flowers are usually wind-pollinated. Wind-pollinated plants face a particular dilemma in that they must rely on the chance contact of pollen from one individual with the female flower parts of another. For this reason, a single pine or alder tree will produce tens of millions of pollen grains during a single season. The surrounding countryside will be dusted with a fallout of the pollen of different wind-pollinated plants during each spring and summer. Most of these grains never reach their intended destination, and are incorporated into accumulating sediments in lakes and bogs, and in other places where dust settles.

The shell of a pollen grain is one of nature's most durable products. It is composed of a unique biopolymer called "sporopollenin". In anaerobic (oxygen free), acidic environments pollen can last indefinitely. To extract pollen from a sample of mud or soil, a palynologist treats that sample with acids so potent that they can easily eat through steel and glass. In this manner virtually all the sediment is dissolved, but pollen grains are left behind unscathed. Of course, the germ plasm within pollen quickly



Pollen grains of a dandelion, Taraxacum. *These are among the most beautifully sculptured types. (Bar=20 microns)*
photo: Dennis Kunkel

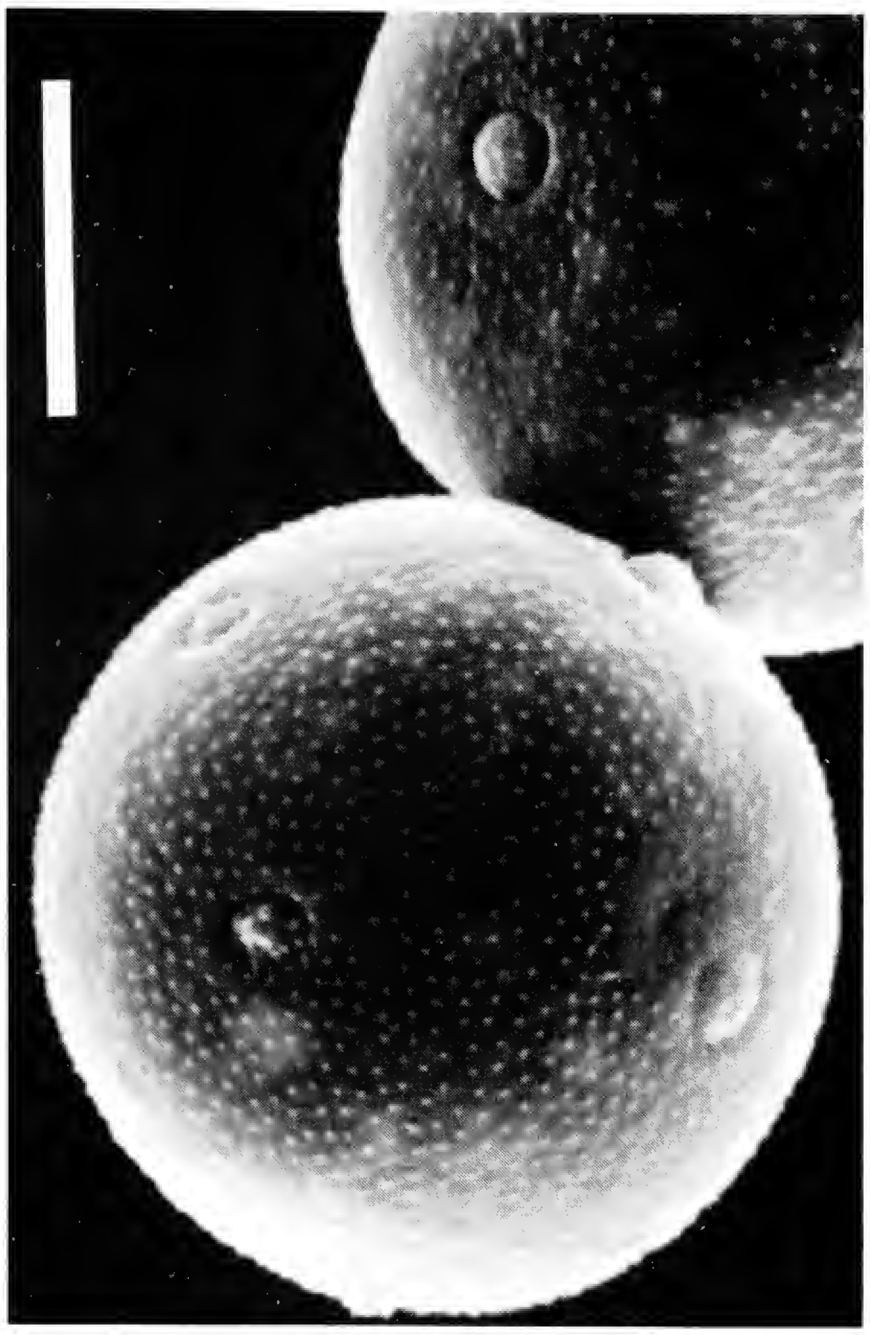
decomposes, and any organic matter remaining is destroyed in the acid treatment process. It is these empty shells that are of value to the archaeologist, for the pollen produced by different types of plants is shaped differently. Some pollen grains, like those of the grasses, are simple spheres. Pine pollen grains have two air bladders that make them aerodynamically lighter and more likely to float great distances on the wind. Others, particularly those of plants that are insect pollinated, sport elaborate patterns of spikes, grooves, ridges, and pores; all at a scale of 10 to 100 microns (1 micron = 1/1,000 of a millimeter).

Palynology has three primary applications to the study of ancient human cultures. It can provide information on the environment of prehistoric man, not only with regard to the type of vegetation surrounding a settlement, but also with regard to how prehistoric agricultural practices affected that vegetation. Since these agricultural practices altered the natural landscape, and since changes in vegetation result in changes in pollen fall-out, the second application of palynology is to provide information on when such agriculture was initiated. The third application is to identify those plants that were food items for primitive peoples, and to determine when a particular food plant was introduced to an area. Organic matter normally decomposes in the soil environment. Therefore the chance that the pollen of a cultivated plant will be preserved in a nearby lake or bog, or in the sediments of the archaeological site, is much better than the chance that the rind or husk of the plant will turn up in the course of archaeological excavations.

Europe has witnessed the most elaborate archaeo-palynological studies, although research efforts by scientists in the New World are now contributing much to our understanding of the agricultural practices and ecological impact of native cultures in this hemisphere. The first discoveries were announced in the 1940's by palynologists studying the vegetation history of western Europe. They were struck by evidence for the rapid decline of certain trees about 4,500 years ago, such as elm, oak, and linden, and the contemporaneous rise in grass pollen and bracken-fern spores and, significantly, a tremendous increase in the amount of charcoal in their samples (charcoal is elemental carbon and is one of the few naturally occurring substances that resist acid treatments used to extract pollen). Following this event, there is increased hazel and birch pollen, as well as the pollen of weedy plants and cereal grains. This pattern is repeated throughout Europe and is now known to have been the result of prehistoric "slash-and-burn" agriculture. As Neolithic peoples migrated through the area they used stone axes and fire to create openings in the primeval forest. These were used for the short-term cultivation of cereal grains and the pasturing of cattle, sheep, goats, and pigs. Hazel and birch, among other plants, were suppressed in the shade of the mature forest. Along with the weeds, these species rapidly expanded when the large trees were destroyed. A final component of this pattern is seen in the disappearance of the pollen of cultivars and weeds, and the partial recovery of the forest. This also is typical of slash-and-burn agriculture; as fertility declines, the fields are abandoned and "secondary succession" of vegetation takes place. A striking aspect of this phenomenon is its widespread occurrence. When one set of fields was abandoned, another set was cleared and, as the human population rapidly expanded, even more extensive areas were altered. There have been no "undisturbed" forests in Europe for at least a millennium, and palynology shows that the disruption of these ecosystems was widespread before the advent of civilization and its attendant technology.

A sure sign of the human hand in this forest destruction is the pollen of cereal grain. These are members of the grass family and, normally, it is difficult to distinguish between different types of grass based on pollen morphology alone. But something extraordinary had happened before Neolithic farmers advanced into western Europe: the genetic composition of cereal grasses had been altered, and this caused an alteration of their pollen morphology. This wasn't the result of primitive gene splicing. Rather, it was evolution caused by the repeated selection of particular types of grasses over the millennia. Grasses with larger and more numerous seed heads that separate easily from the stalk were repeatedly chosen from wild populations with smaller, more persistent fruit. This process was unintentional. Primitive hunter-gatherers were not seeking to breed productive strains of cereal grasses so they could settle down and become farmers. It merely reflects the result of preferential harvesting over thousands of years, and the fact that the seeds that were harvested stood a good chance of being dispersed and reseeded as a result of human activity. So, by the time Neolithic farmers spread into Europe, they carried with them a stock of cereal grains that had distinctive pollen morphologies. And archaeologists, working in concert with palynologists, have been able to trace the timing of introduction of these and other critically important food plants throughout the world. For example, by such methods the introduction of corn from Central America has been traced through the prehistoric cultures of North America. Corn produces the largest pollen grain of any cultivar; it is frequently more than 100 microns long. Its large size makes it ill-suited for wind-dispersal and, like many cultivated plants, it is dependent on man for its continued existence.

A mistake occasionally made by archaeologists is to present a series of soil samples from a "dig" to a palynologist, and request that the palynologist study the pollen flora therein, and from those studies reconstruct the vegetation that prevailed. The palynologist will then explain that this cannot be done. Why? There are two reasons. Paradoxically, highly durable pollen grains are rarely preserved in the soil environment of open-air sites. There are types of soil fungi that digest pollen, and leave nothing behind except fungal spores. In the Mid-West and East, pollen from archaeological sites has been recovered only rarely, and usually from soil samples taken immediately adjacent to copper artifacts. The copper sulfates produced by the weathering of these artifacts sterilize the nearby soil, and prevent the growth of pollen-destroying fungi. The second reason has to do with the ecological impact of human beings. In regions where the soil is sufficiently dry or acidic to allow pollen preservation, such as in



Pollen grains of a plantain, Plantago. *Although usually listed as wind-pollinated, the genus has some species where specialized syrphid flies can also do the job. Insect pollination in* Plantago *was discovered very late because the syrphids involved are very early risers and have finished their work by the time the lazy biologist appears on the scene! (Bar = 10 microns)*
photo: Dennis Kunkel

parts of the West, the pollen of local weeds dominates samples from archaeological sites. Any permanent human habitation, be it prehistoric or modern, is the site of trampling, settlement clearance, wood harvesting, and other activities that favor weeds. And, so-to-speak, the palynologist cannot reconstruct the forest for the weeds. Productive samples from sites in the Mid-West and Southwest are usually dominated by Chenopodiaceae (goosefoot, pig-weed, or saltbush family) pollen. Those from coastal California usually yield very high percentages of Asteraceae (sunflower family) pollen. So, when seeking to define the type of vegetation in which a prehistoric culture lived, the palynologist will select a nearby bog or pond and take a sediment core from near its center. The mud samples from that core provide the fossil pollen on which to base a vegetation reconstruction, based primarily on the record provided by wind-dispersed pollen grains. Since the mud settles year-by-year in layers, vegetation reconstructions for the time before, during, and after human habitation can be made by sampling successive layers from the core. And, because the environment in the bottom of a pond is largely oxygen-free and acidic, the fossil pollen is well-preserved.

Recent research indicates that the plants we term "weeds" were frequently harvested, and played an important role in the subsistence strategies of certain prehistoric cultures. Carbonized pig-weed (*Chenopodium*) seeds from Mississippian (ca. 1000 to 1400 A.D.) villages in the Mid-West display the enlargement typical of cultivated plant species, like the cereal grasses in Europe. Pollen in mummified human feces from dry caves and Southwestern pueblos reveals a varied diet that included plants in the pig-weed family, and also bee-weed (*Cleome*). A future challenge to the palynologist and archaeologist lies in the comprehensive characterization of pre-Columbian, native weedy floras. Most of our garden-variety weeds are thought to have been introduced from Eurasia. What species made up these prehistoric weedy floras, and how were their niches preempted by species introduced at the time of European settlement?

Perhaps the greatest long-term contribution that palynology and other paleoecological studies have made to the understanding of prehistoric man has been to illustrate the tremendous ecological impact that humans have on the environment. Widespread ecological destruction did not start with the rise of classical civilizations. This idea is not particularly popular with many people, for it discredits the attractive image of primitive man as a "noble savage" who was "in tune" with his environment. Instead, it shows that humans have always been capable of widespread environmental damage in their quest for food and shelter. And it explains the fall of ancient civilizations, ranging from the Anasazi of the Southwest to the high culture of Easter Island, by simple resource depletion. The larger the human population, and the more sophisticated its technology, the more extensive was the destruction of natural ecosystems upon which it ultimately depended. Thus, an important lesson can be learned from the palynological and archaeological record, one that applies directly to our own time.

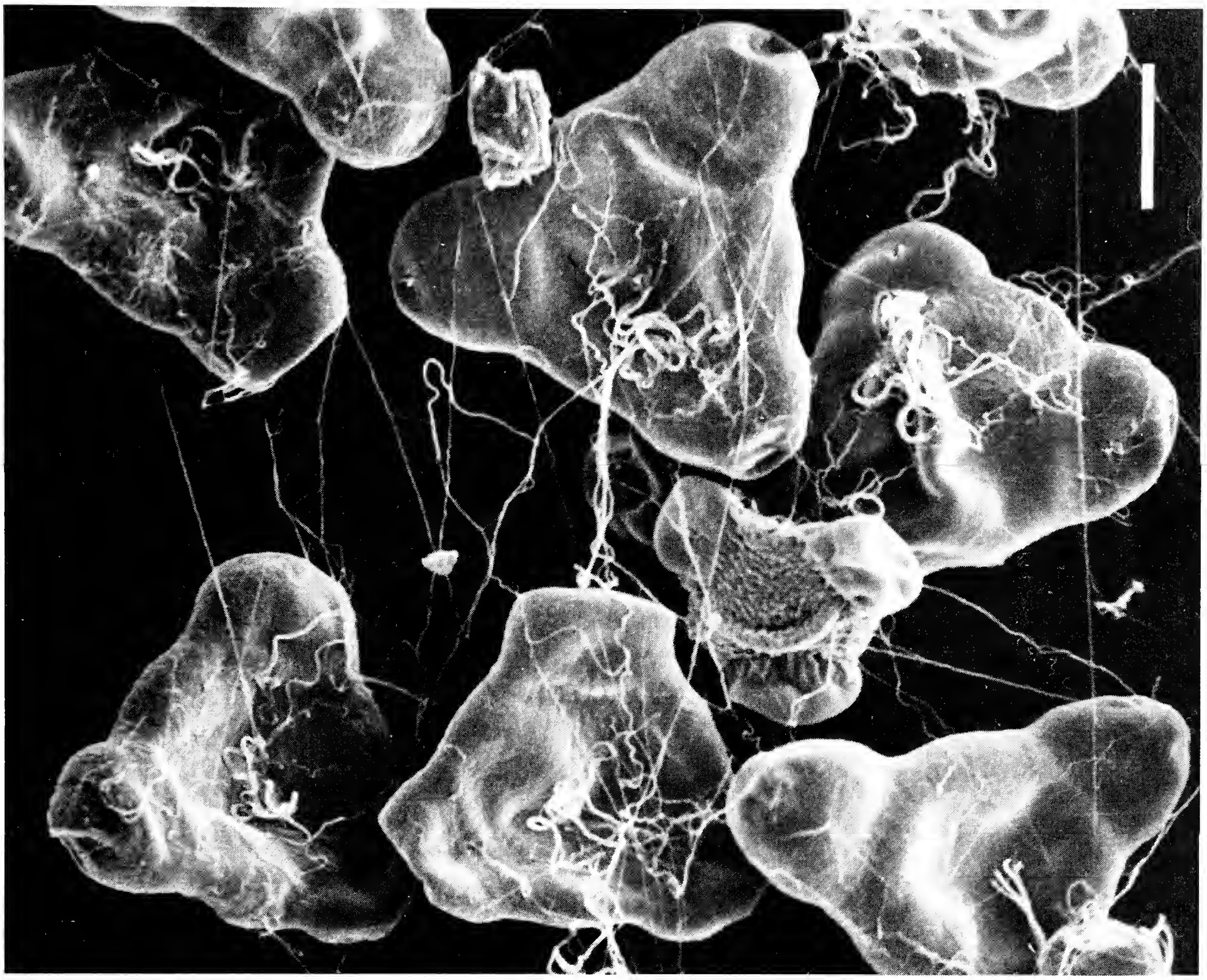
Flower-birds and Bird-flowers

Part I

BASTIAAN J. D. MEEUSE

In Europe and the United States, most people associate flowers with bees and butterflies. However, in tropical countries and in Australia, birds may be *at least* as important as insect pollinators. The examples of mutual adaptation between flower and pollinator are equally fascinating in both cases. All in all, there are about 2,000 species of birds, belonging to about 50 families, that visit flowers more or less regularly. About two-thirds of these customers are specialists, relying on flowers as their most important, or even their only, source of food. In America, such specialists are the hummingbirds (Trochilidae), with more than 320 species in 123 genera, and in Hawaii the honey-creepers (Drepanidae). In the region of Australia and New Guinea we find such queer customers as the honey-eaters (Meliphagidae) and the brush-tongued parrots (Trichoglossidae). In Africa and Asia, finally, there are several groups of birds with flower-loving representatives, such as the nectar birds (Nectariniidae) and the spectacle birds (Zosteropidae). As to the flowers that cater to birds: of the 300 families of flowering plants, a good one-third have at least *some* members with flowers that appeal to birds (so-called ornithophilous flowers). A real paradise for flower-birds is Australia, where more than 100 bird species are involved with more than 1,000 species of plants. Bird-pollination in this part of the world must be very old indeed, for in some genera found only in Australia *all* the species are bird-pollinated. Some biologists go so far as to say that in regions such as Central and South America, birds, rather than insects, have been the major agents in creating the colorful host of tropical flowers in the long, long process of evolution.

It is conceivable that bird-pollination got its start in hot climates when the birds began to visit flowers to quench their thirst with nectar. This idea may go back to Rumphius, that stout-hearted blind seer who reached the Moluccas (the Spice Islands in eastern Indonesia) around 1650 and who has left us a description of how certain parrots came to the coral tree, *Erythrina indica,* to drink the "dew" (the nectar!) which accumulates in the blossoms. Each single flower contains about a thimbleful of the sweet juice, and in the dry season each tree is, for months on end, covered with countless blooms. Rumphius was not aware of the birds' role in pollination; he was



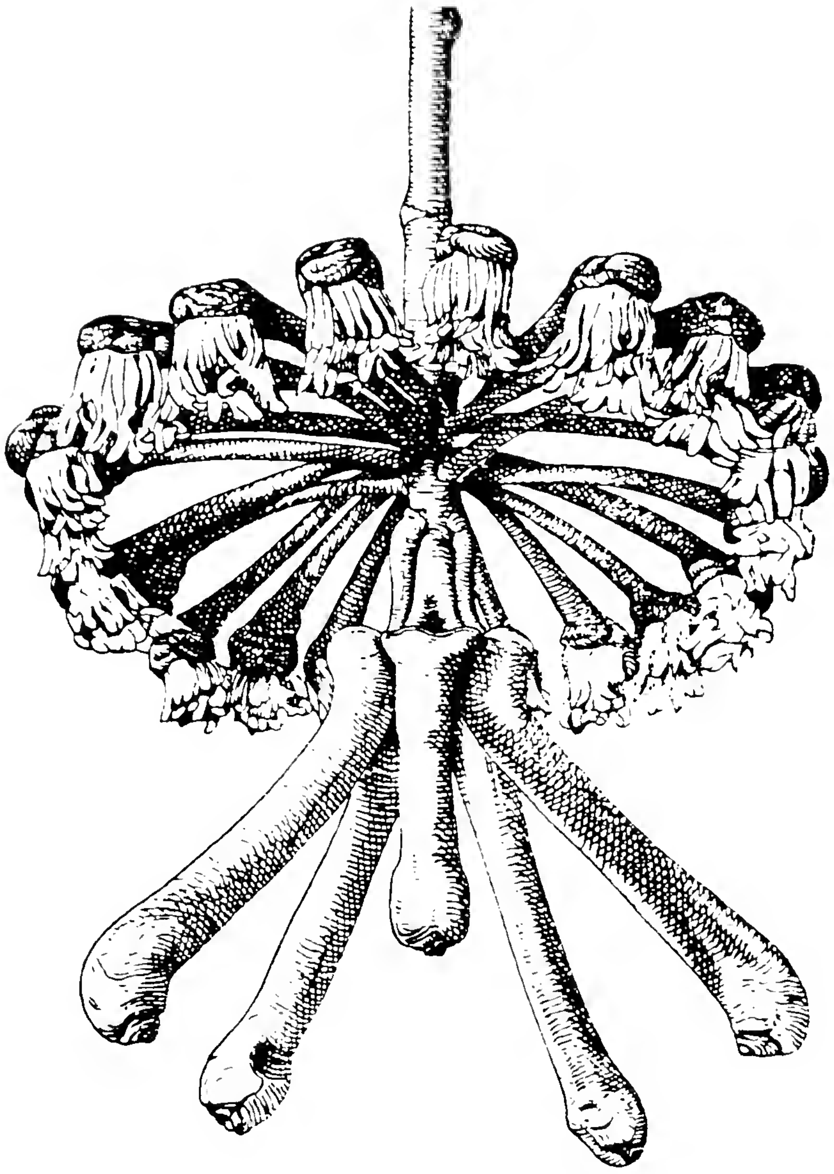
Pollen of bird-of-paradise flower, Strelitzia *Dispersed by birds (but not birds-of-paradise!). The grains, which are very large and perfectly spherical, are connected to one another by sticky threads. (Bar = 100 microns)* *photo: Dennis Kunkel*

born too early for that!

Things were not seen in the proper light until 1874, the year when T. Belt published his book *The Naturalist in Nicaragua* and described, in it, the flower (actually an inflorescence) of *Marcgravia nepenthoides* which he thought was bird pollinated. The amount of nectar, which in this case accumulates in five special pouches, is indeed impressive. The same can be said for the flowers of the spear lily (*Doryanthes*) each of which can produce a liqueur-glass full of nectar. In South Africa, the native *Protea mellifera* is locally known as "suikerbossie" or sugarbush because the nectar is so abundant that it can easily be shaken out of the flowers as a sweet rain; in Cape Town markets, this nectar used to be sold in jars as cough syrup. Similar to *Protea mellifera,* in terms of sweet rain, is red-hot poker (*Tritoma* or *Kniphofia*), another South African plant which residents of the Pacific Northwest can now admire in their own gardens. Although in its native country it is pollinated by sunbirds, we can give it a *very strong* recommendation as a hummingbird attractant! Other common visitors of *Kniphofia* are honeybees, and one can easily see why Australia, where bird pollination is common and honeybees were originally absent, has become a paradise for beekeepers.

Characteristics of bird-pollinated flowers

Birds have excellent vision but a very poor sense of smell. In contrast to bees and many other insects, which are red-blind, they see red as a color; in fact, there is evidence that red is especially attractive to them. At least *some* hummingbird species can also see ultraviolet as a color. It stands to reason that a flower which is attractive to birds has characteristics which are different from those of a bee-flower (which

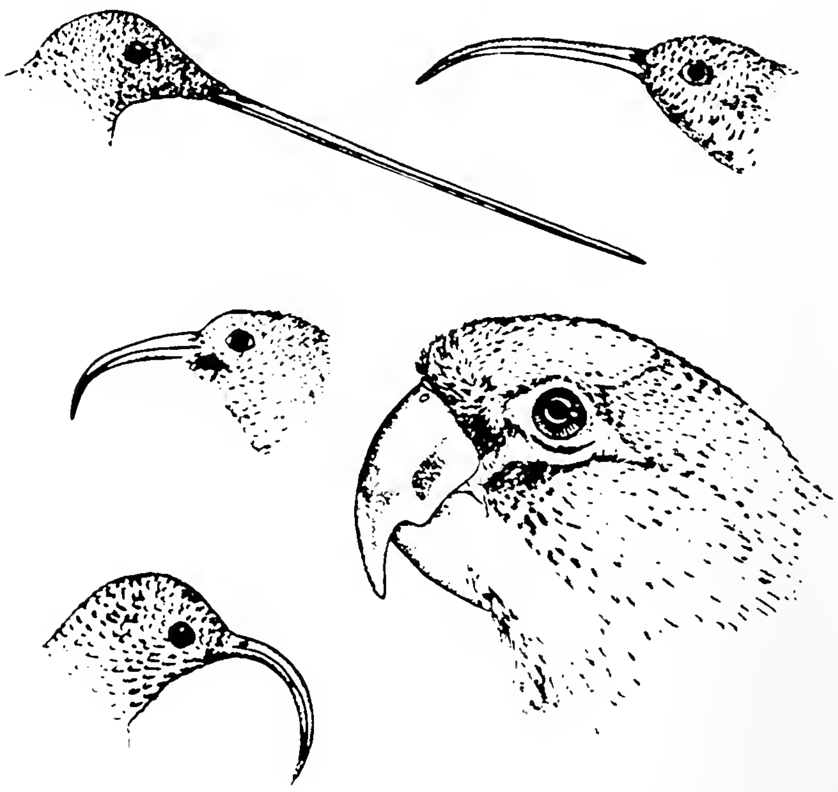


Inflorescence of Marcgravia *from Central America. Birds are the normal pollinators, but bat-pollination is suspected in a few cases.* *From* The Story of Pollination *by B. J. D. Meeuse (1961).*

commonly has a minty odor) or a flower pollinated by butterflies (which possesses a sweet fragrance and a *very* narrow corolla tube). Is it possible, then, to come up with one special, single type which we could describe as "the" bird-flower? The answer is: yes and no. Birds are highly developed animals which behave in a much more "intelligent," or at least in a less rigid, way than insects do. Their versatility and flexibility make it possible for them to encroach upon the pollination niche of other creatures, e.g., bees. This leads to the sharing of flower resources in the landscape by birds and other pollinators.

In our area, such plants as red flowering currant (*Ribes sanguineum*) and salmonberry (*Rubus spectabilis*), which are served by both bumblebees and hummingbirds, demonstrate the phenomenon very neatly. In a few cases, sharing may cause the hummingbirds to come to grief, for instance when they compete with the small *Trigona* bees for the flowers of *Centropogon* in Central America. The bees operate in large groups and will ferociously defend "their" flowering shrubs against invading hummers!

Still, in spite of resource sharing, there are a few flower species that are so highly specialized for bird pollination that they can discriminate against insect visitors with great effectiveness; they can thus be regarded as representing *the* typical bird-pollinated flower. Not surprisingly, one of our best chances to find the "bird-flower" is to seek it in the group of plants served by the most specialized avian pollinators, the hummingbirds. The *Fuchsia* flower is one of the most illuminating examples. It is completely odorless and its position is pendent. Since hummingbirds feed while on the wing, they need no landing platform. In contrast, plants such as the monkeyflowers (*Mimulus*), and those in the mint family, the Labiatae, offer a well-developed "lip" of the corolla, used by bees as a landing platform. *Fuchsia* flowers are available in the daytime, and their buds do not open *only* in the evening, as so many hawkmoth-pollinated flowers do. Most wild fuchsias have red flowers that produce an abundance of thin nectar—thin, perhaps because the hummingbirds would have trouble sucking up a thick fluid, but perhaps also because bees appear to shun thin nectar, giving birds a virtual monopoly in some cases. The whole flower is sturdy, stamen and pistil are straight and strong, and the ovules (the prospective seeds) are kept out of harm's way in an inferior ovary, as a defense against the probing bill of the pollinator.

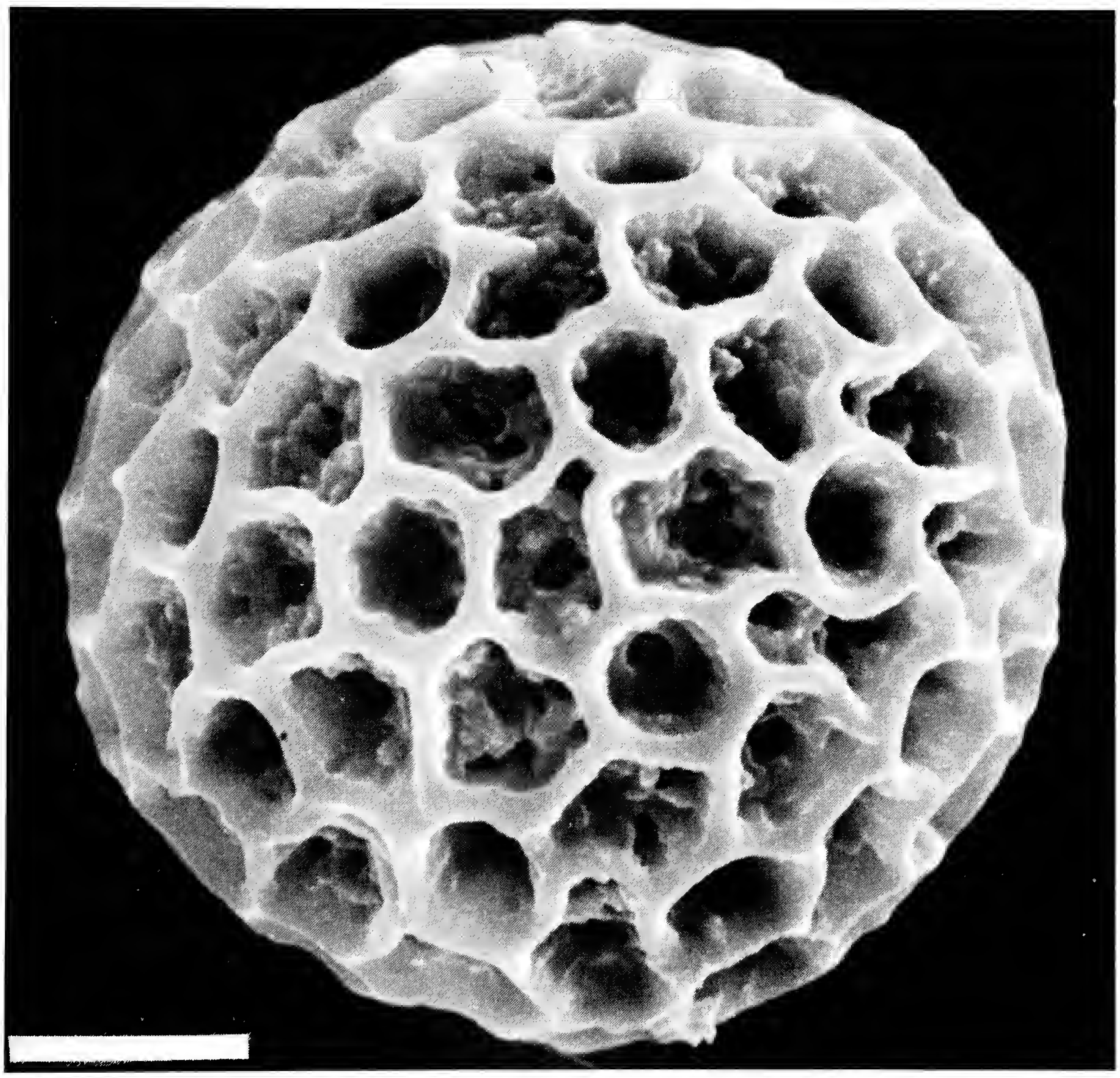


Bill shapes of various nectar-eating birds, and of a parrot. *From the Oxford/Carolina* Reader *on pollination by B. J. D. Meeuse. Courtesy of Oxford/Carolina Biological Supply Company.*

Flowers of Ribes lobbii. *Excellent imitators of Fucshia flowers.* *photo: author*

Fuchsia flowers have their imitators, even in our state of Washington where the genus is not native. A most charming example is *Ribes lobbii,* which belongs to an entirely different family. It is an almost incredible case of convergent evolution, which seems to lend some support to the facetious (but famous) statement that ''morphology is nothing but crystallized ecology''! Indeed, the *R. lobbii* flowers, which are bird pollinated, look completely different from those of most other *Ribes* species, which cater to flies and bees.

Hummingbirds are found only in the Americas. In other parts of the world, flower-birds like to have a perch (for instance, a twig) to sit on while they are feeding, or they come down for a landing on the flower itself. The spectacular South African bird-of-paradise plant (*Strelitzia reginae*), often grown in greenhouses and also common in the parks of Los Angeles—where it is the official flower—is an example of the latter method. Shape and coloring, in combination with the large size of the *Strelitzia* flowers, have led people to see in them a resemblance to some exotic bird with golden wings, ready to take flight. No insect is strong enough to push its way past the median petal of the blossom, which blocks the way towards the nectar; only birds can do the job—in South Africa mostly sunbirds (*Nectarinia* species). Hovering near the flower to get at the nectar, the pollinator's breast or belly will inevitably push down, left, and right on the corolla lobes, which open up like two halves of a door and expose the pollen which in a mature flower has come out of the anthers and is lying hidden in the belly of the lobes. The pollen grains, perfectly spherical and exceptionally large (0.12 to 0.14 millimeters in diameter) are connected to one another by sticky and wavy threads,



Pollen of cup-and-saucer vine, Cobaea scandens. *The direct ancestors of this garden plant, which were tropical, were bat-pollinated.*
(Bar = 20 microns)
photo: Dennis Kunkel

Flower of Strelitzia, *bird-of-paradise being pollinated by a white-eye bird,* Zosterops pallidus.
photo: George Bernard of Oxford Scientific Films.

often twisted into a cobwebby tangle. The pollen masses attach themselves easily to the bird's feathers and can then be carried to another *Strelitzia* flower where they may be deposited on the exserted pistil tip, achieving cross-pollination.

A number of ornithophilous flowers, for example, those of *Loranthus* (a tropical mistletoe) are explosive and cover their visitors thoroughly with pollen. Some South African and Australian plants that cater to birds produce their flowers close to the ground. In Australia, these are served by wattlebirds, which have the habit of drinking while standing up and like to hop from flower to flower.

The question whether or not flower-birds really have a preference for red and orange colors has been the subject of much debate. P. Raven has argued that bees (red-blind) see red as black, so that redness of a flower "pre-empts" it for birds. On the other hand, it has been pointed out that many birds have in their retina (the sensitive area in their eyes) a multitude of minute fat droplets of a deep orange color. Together, these act as a light filter, so it could be said that hummingbirds look at the world through rosy spectacles. Orange and red rays coming from the environment will not significantly be interfered with, but green rays that reach the bird's retina from (e.g.) a leaf-bearing tree will be absorbed almost totally before they can create any nervous impulses that in the brain could be recorded as "color." A holly tree bearing red fruits will show great contrast to birds; the red will stand out conspicuously against a background which is perceived as dark grey! In his book *Hummingbirds,* Walter Scheithauer tells us about one particular little hummer that was allowed to fly around freely in his room. It would inspect all the colorful objects and color spots, paying special attention to red ones. It seemed fascinated by the mouth of his young daughter, and tried repeatedly to insert its bill between her red lips! The girl considered herself fortunate that her little visitor was not a specimen of the sword-bearing hummingbird (*Ensifera ensifera*) which has a bill like a knitting needle, straight and sharp and about as long as the bird itself.

Ecological importance of red in the flowers of scarlet gilia

That red colors must somehow be very important in a hummingbird's life has recently been demonstrated beautifully in still another way by Ken Paige and Thomas Whitham, biologists at Northern Arizona State University, with populations of scarlet gilia (*Ipomopsis aggregata*) growing on Fern Mountain near Flagstaff, Arizona. Although at sea level the flowers of scarlet gilia are indeed bright red, those produced by the plants growing on Fern Mountain showed a consistent change in color, ranging from red to pink to white, through the flowering season, which lasted from July to early September. This color change coincided neatly with a shift in the composition of the pollinator population. Scarlet gilia relies mostly on two types of visitors for its pollination: hummingbirds and hawkmoths. At higher elevations, the birds (which have a preference for red) are predominant early in the season. They leave the area in August, but then are largely replaced by hawkmoths. These animals forage at night and selectively pollinate the light-pink and white flowers. The color shift is not just based on the fact that early-blooming gilias produce mostly red flowers, and late-blooming plants pink or white ones; even individual plants show a color shift in the flowers they successively produce. At lower elevations the composition of the pollinator population does not change markedly during the flowering season, and the relative constancy of the flower color corresponds nicely with this observation. Incredible though it may sound, the chameleon-like behavior of scarlet gilia at higher elevations appears to make it possible for this plant to accommodate its pollinator population throughout the flowering season, thereby improving seed-set and the chances of the species to survive.

More to Come

In the fall issue, Part II will continue with its emphasis on hummingbirds!

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New On The Shelf

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VALERIE EASTON

If you want,to learn more about pollination, there are two interesting new books in the library on the subject. . .

The Sex Life of Flowers. Meeuse, Bastiaan and Morris, Sean. Facts-on-File, 1984.

The great degree of genetic variation between one generation and the next, which is the advantage of sexual reproduction, applies to plants as well as to animals. However, plants cannot move about to facilitate reproduction as animals can, so they must use the borrowed mobility of animals, wind and water to move their pollen grains between flowers. An amazing variety of pollination methods have evolved, and these are fully described and beautifully photographed and illustrated in this fascinating account of how flowers reproduce.

How Flowers Work, A Guide to Plant Biology. Gibbons, Bob. Blandford Press, 1984

Written by a botanist and photographer, this volume explains how flowering plants grow, develop and reproduce, and how they fit into the plant kingdom as a whole. Line drawings and wonderful color photographs, along with an informative text, illustrate how the plant obtains food and water, as well as the processes of respiration and transpiration, vegetative and sexual reproduction, pollination and seed distribution.

Other New Books

American Rock Garden Society and Denver Botanic Gardens. *Rocky Mountain Alpines*. Prepared for Alpines '86, Second Interim International Rock Garden Plant Conference, Boulder, Colorado. Timber Press, 1986.

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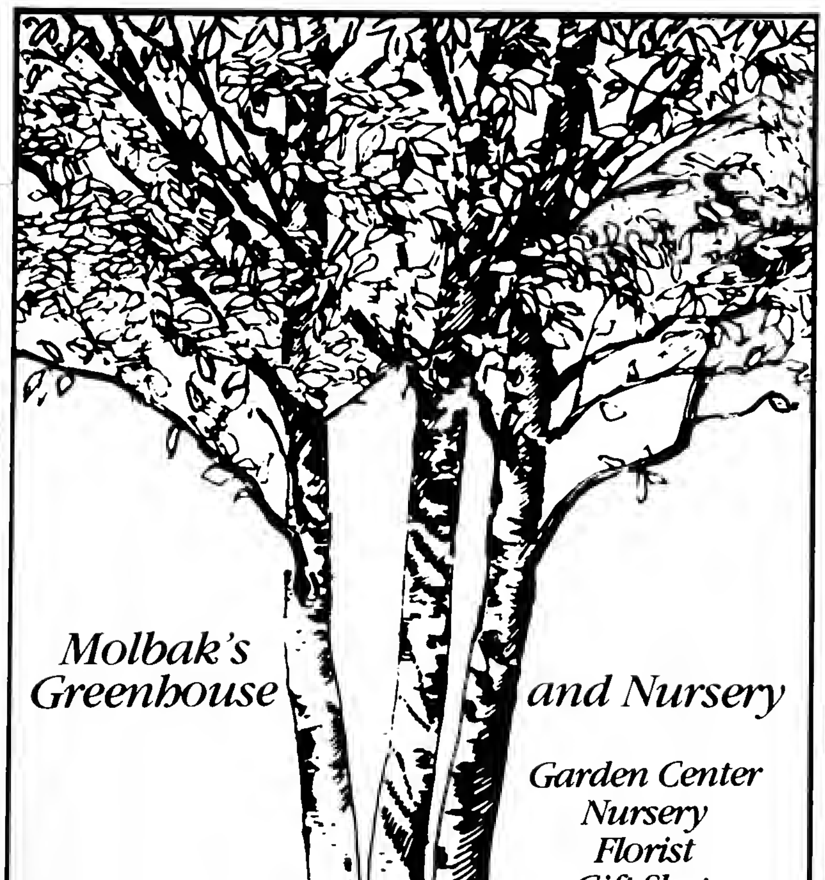
Special thanks to the individuals and organizations who have contributed these books to our library.

All of these books can be found in the Elisabeth C. Miller Library, Center for Urban Horticulture, 3501 N.E. 41st Street. The library is for reference use only; a copy machine is available for public use. Hours are 9-5 Monday through Friday.



I.M.S. Grant for Arboretum

The federal Institute of Museum Services has awarded the Arboretum a grant of $51,163 for general operating support during fiscal year 1987-88. The Arboretum was one of five Seattle-area museums to win the award, which provides valuable funding for day-to-day operations. This year 1296 museums nationwide competed for 409 grants, only 12 of which went to Arboreta/Botanical Gardens. "Those museums receiving awards," says I.M.S., "have demonstrated the highest standards of services and operations." Congratulations to Joyce Brewster for putting the proposal together, with substantial help from Director H. B. Tukey Jr., Curator Timothy Hohn, Professor Clement Hamilton, and other members of the Arboretum management team.

This is the fifth I.M.S. grant awarded to the Arboretum in recent years and will bring total funding from that source to $197,360. An additional proposal for conservation support is still pending.

Pollen grains of a forget-me-not species, Myosotis. *These are among the smallest types known, even though the plants are not wind-pollinated but are served by various bees. (Bar = 5 microns)*
From: Pollen Grains by Electron Microscope, *Kunkel and Meeuse, page two.* *photo: Dennis Kunkel*

Published by the
Arboretum Foundation
Washington Park Arboretum
University of Washington XD-10
Seattle, Washington 98195

MRS H.P. CLAUSING
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